

# ECOLOGICAL MONOGRAPHS



VOL. 13

OCTOBER, 1943

NO. 4

OFFICIAL PUBLICATION OF THE ECOLOGICAL SOCIETY OF AMERICA

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PUBLISHED QUARTERLY BY DUKE UNIVERSITY PRESS  
DURHAM, N. C., U. S. A.

# ECOLOGICAL MONOGRAPHS

A QUARTERLY JOURNAL  
FOR ALL PHASES OF BIOLOGY

Issued on the fifteenth of December, March, June, and September

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Agents in Great Britain: The Cambridge University Press, Bentley House, 200 Euston Road, London, N.W. 1. Prices can be had on application.

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## THE PLANT LIFE OF CUBA

WILLIAM SEIFRIZ

*University of Pennsylvania*

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# THE PLANT LIFE OF CUBA

## I. INTRODUCTION

### 1. FOREWORD

A study of the plant life of a country offers several possibilities as to plan and procedure. There is the taxonomical approach with its lists of plants. In contrast, a physiological study introduces atmometer readings, soil analyses, and pH determinations. Still another procedure is that of geographical botany which rests on broad climatological, topographical, and geological data. A geographical study of the plants should precede one on the physiological causes thereof, that is to say, descriptive phytogeography is the background for experimental ecology.

The progress of ecology has been that common to every science; first the recording of obvious and general facts, then a careful analysis of local conditions, and finally, experimental work. The ecology

of Cuba has not yet reached a completion of the first stage, and until this is done detailed research cannot be fitted into a general scheme. The present survey of the vegetation of Cuba is primarily a geographical one. It is offered not only for its own intrinsic value, but as a background for future work.

It is the writer's hope that physiological and ecological studies in the tropics will greatly increase. Both of these sciences are based on studies done primarily in temperate, especially north temperate, countries. Consequently, theory and practice, terminology and research, all rest on the behavior of vegetation accustomed to freezing and winter hibernation which a tropical plant has never experienced. And the northern plant, in its turn, has rarely endured a prolonged drought or excessive humidity such as the tropics have to offer. No classification of plants, no laws of physiological behavior, and no ecological principles can be regarded as final or all inclusive if they do not fit one region as well as another. If general laws cannot be formulated, they must then be stated as holding only for the region on which they are based. The ecology of plant life in the north presents so many difficulties when applied to tropical countries that botanists there are inclined to ignore it and deny many of its concepts. How can we, they say, apply a principle such as that of plant succession which ends in climax associations of pure stands when these are rare in the tropics.

Plant succession and climax associations are as real in the tropics as in the north. Pure stands need not come into the picture. The general rule seems to be, abundant species with few individuals of each in the tropics, and few species with many individuals of each in the north.

### 2. ACKNOWLEDGMENTS

No thorough account of the plant life of Cuba could be written today without the cooperation of the Island's foremost botanical scholar, Hermano León. Only two major trips have I had in Cuba without the able guidance and delightful companionship of Brother León. Dr. R. H. Palmer has also been of great assistance to me in various ways. My debt to him is represented primarily by the geological section of this monograph. It is based on a longer account, now in press, by Dr. Palmer. To several other botanists am I grateful, particularly Mr. E. P. Killip and Mr. E. C. Leonard of the U. S. National Museum at Washington, who have identified many plants collected by me in Cuba and on other Caribbean shores. To Mr. José Carabia I am also indebted for much information on Cuba.

### 3. NOMENCLATURE

The function of words is to convey ideas. Any system of nomenclature which does not fulfill this



FIG. 1. *Spathelia brittonii* on a mogote at Sumidero.

function fails in its purpose. If an idea is given a name, the concept is more easily retained. So we face a dilemma, that of naming every concept in order to give it a place in a system of nomenclature, and the opposing policy of keeping terms down to a minimum. Personally, the writer inclines toward a minimum of terms and definitions. There is a finality about definitions which retards thought. He will, therefore, forego rigid definitions of common ecological terms. The difficulty in arriving at a consensus of opinion on so well recognized an expression as "association" shows how flexible definitions may be in a science yet too young to have a rigid terminology. Many excellent concepts in ecology would, I believe, have been more widely accepted had they not been lost in a sea of new words.

In spite of disagreement on the precise meaning of terms, most of them present no difficulties. Thus, "association" serves well to indicate a specific group of plants, whether large or small. Other equally familiar ecological expressions, such as xerophyte, mesophyte, and halophyte, are clear. But difficulties there are, and they occur in some well-recognized terms in common use; among them are zone, savana, and desert. The meaning of these and others is best discussed where the term is first used. But there are several questions on which the writer must at the outset take what he hopes is a not too drastic stand. These are the matter of capitalization of specific names, and the proper selection and spelling of generic names.

As for the first question, the writer will adopt the policy which, fortunately, is coming into vogue, that of writing all specific names with a small initial letter. It is now the accepted policy among zoologists. A vast amount of work and worry for the non-taxonomic botanist is thereby saved and but little information of value is omitted.

The proper selection and spelling of generic names is a more difficult question to answer.

The adoption or rejection of new plant names should be a matter of international agreement; unfortunately, it is often a personal matter. Americans have accepted the renaming of *Oreodoxa* to *Roystonea*, but many English botanists in the British West Indies retain *Oreodoxa*, which the writer too prefers, but scientific opinion is now overwhelmingly against the old name. He is even more reluctant to accept *Delonix* for the royal poinciana. A number of botanists have made frequent and earnest pleas for the retention of familiar plant names of long standing, even though they sometimes stand in opposition to the rule of priority. As a result we now have a long list of *nomina conservanda*.

In many instances a final decision has been reached, but what of *Coccolobis* for *Coccoloba*? These are matters for the taxonomist. The ecologist and phytogeographer have naught to do but follow and obey. Yet, the writer has, so far as possible, retained old and familiar names, especially where the new name has not received international recognition, or where

confusion and uncertainty are so great as to justify any one of several recognized names; thus, the saman or rain-tree has suffered many vicissitudes at the hands of botanists, having lived through *Inga*, *Pithecellobium*, *Pithecellobium*, and *Samanea*.

Also troublesome, particularly in reference to Puerto Rican plants, is the use of two codes, the American and the International. In the main, I have kept to the International code and ignored the Britton-Coville system of nomenclature. Engler and Prantl's *Pflanzenfamilien* has served me as the final authoritative reference.

The proper spelling of plant names is a less serious but important question. The genus *Cinchona* was misspelled by Linnaeus, either unknowingly or intentionally for the sake of euphony. This misspelling of the name of the Countess of Chinchon, though recognized, was never changed or questioned, but the erroneous spelling of Plumier's name by Linnaeus has been questioned, changed, and changed back. When the matter of *Plumeria* came up in the preparation of this manuscript, the writer asked for opinions and was told that as Plumier was the French botanist after whom the tree had been named, it should be *Plumiera*. But others maintained that Linnaeus wrote it *Plumeria* and one does not correct Linnaeus. To this, objection was raised on the ground that the Vienna code permits an obvious typographical error to be corrected even when made by Linnaeus, which would make the genus *Plumiera*. There then appeared a monograph on *Plumeria*, and this settled the matter in Linnaeus' favor, but not as Plumier would have liked it. The question really is whether or not Linnaeus' error was intentional, and that we shall never know. The decision in favor of *Plumeria* is confusing for it gives us the genus *Plumeria* and the species *Tovomita plumieri*, both in honor of the same man, Plumier. However, although I prefer *Plumiera* for the sake of uniformity and etymological accuracy, the matter is settled in favor of *Plumeria*.

#### 4. BIBLIOGRAPHY

Published works on the plant life of Cuba are few. Hermano León (1926, 1936) has published two articles on the phytogeography of Cuba: one, "Flora de Cuba," is in the encyclopaedia "Libro de la Cultura"; the other, entitled "Cuba," is in "The Naturalist's Guide to the Americas" (León 1926). The latter deals with the geology and animal life of Cuba as well as the vegetation. Mr. Carabia (1940) has a "Brief Review of the Cuban Flora" in *Chronica Botanica*. A very useful general work on the flora of Cuba is Jan Thomas Roig's (1928) "Diccionario Botanico."

There is no published taxonomy of Cuban plants, though one has long been promised. The nearest approach to it is the *Symbolae Antillanae* of Urban, based on the collections of that extraordinary collector Dr. E. L. Ekman.

The only full presentation of the plant life of Cuba with an ecological flavor is the delightful ac-

count given by Frère Marie-Victorin and Hermano León (1942) in their book, "Itinéraires Botaniques dans l'Île de Cuba." A second volume is to follow.

No account of the plant life of any of the West Indian islands could be satisfactorily given without frequent reference to the vegetation of other Caribbean lands. This is particularly true of Cuba, the vegetation of which is closely affiliated with that of Haiti, Venezuela, and Yucatan. As one goes south and east along the Antillean chain to Puerto Rico, Martinique, and Trinidad, plant relationships with Cuba become less and less pronounced, yet certain general vegetational features characterize all the American tropics. Type species and endemics differ, but the facies are similar; strand, thicket, and mountain forest are much the same in general character throughout the Caribbean circle.

The nearest land off Cuba's shores is Haiti, fifty miles away. A comparison of the two islands is, therefore, particularly instructive. For this purpose, the volume by R. Ciferri (1936), "Studio Geobotanico dell'Isola Hispaniola" is excellent. For nearby Jamaica, Forrest Shreve's (1914) ecological "A Montane Rain Forest" is also very good. Useful is the taxonomic work, "Flora of the British West Indian Islands," by A. H. R. Grisebach (1864). For the American islands there is N. L. Britton's (1924) "Flora of Porto Rico and the Virgin Islands." For the French islands, there are the taxonomical and ecological accounts by H. Stehlé (1935), "Flore de la Guadeloupe et Dépendances." The mainlands of northern South America and Central America are the original homes of Cuban plants; comparison of their floras is, therefore, particularly instructive. Chief among the published accounts of the vegetation of continental Caribbean shores are H. Pittier's (1926) "Manual de las Plantas Usuales de Venezuela," and Paul C. Standley's (1928, 1931) floras of Panama, Honduras, and Yucatan. Standley's floras are the most recent and complete of Central America. For northern Colombia, the writer's (1937) "Die Höhenstufen der Vegetation in der Sierra Nevada von Santa Marta" is the most recent botanical account of this region. The greatest of all historical publications on tropical American plant life in the Caribbean region is Oviedo's (1535) "La Historia Natural y General de las Indias."

##### 5. PLAN

The geographical description of a country's vegetation may follow the route of a real or imaginary journey. For Cuba, either would be a very convenient way, the island is long and narrow and a traveler must of necessity go from east to west, or west to east. Such a procession of vegetational types is the one usually experienced in the field, and for this reason it has a greater fascination than other more orderly procedures, but it is not sufficiently methodical for a geographical study. I shall, therefore, not follow an imaginary journey, but rather combine and summarize the results of my several sojourns on the

island grouping the information under ecological types. Such a description will possess unity, without digressing far from geographical continuity.

Another question to be settled in planning a study of vegetation is that of the relative emphasis to be placed on taxonomy, morphology, physiology, habitat, topography, and physiognomy. Schimper called his master work, "Plant Geography on a Physiological Basis," thus laying emphasis on physiology. But a phytogeographical account may rest on other vegetational features. One of these is the general appearance, or facies, of a land when viewed from afar, without regard to the responsible factors. Such a study would be physiographical. Still another basis of ecological study is that of plant types or growth forms. One may thus imagine some half dozen kinds of descriptive ecology, each based on, or correlated with, characteristics of the vegetation or the environment. But they are not as distinct as usually imagined, for whatever trend the study of the subject may take, it of necessity involves the others. Thus, physiognomical ecology is in part based on topography. It likewise involves taxonomy and morphology. One cannot describe a vegetation without naming the plants, and the words used to describe the plant groups are often morphological terms, such as forest and thorny bush. Physiology is always involved in any but a pure taxonomical or morphological study, for the appearance of land expressed in terms of its plant life is determined by the physiology of the plants involved. Because Warming failed to realize this, he made the erroneous statement that a purely physiognomical study is "devoid of scientific significance, which is introduced only when physiognomy is founded upon physiological facts." The statement is not only untrue but meaningless, for physiognomy owes its character to physiological conditions.

It is a physiognomical ecology of Cuba that will be given here.

In the fulfillment of this plan the vegetation of Cuba has been divided into nine major associations:

1. Coast
2. Desert
3. Thicket
4. Limestone
5. Savana
6. Cultivated lands
7. Communities and Guilds
8. Forests
9. Alpine vegetation

To these a final chapter has been added on Maisi, at which locality there are, within a relatively short distance from coast to mountain top, five distinctive plant associations, each restricted to a mesa or terrace, and each typical of a part of Cuba. Maisi thus serves well as a final chapter, for it is a survey of the plant associations of all Cuba.

The writer will also adhere wholly to his own experiences in Cuba, describe only land upon which



he has trod. Though this plan will leave some regions unmentioned, it will leave no major feature of the island's vegetation undescribed; and such is the purpose of this monograph, to depict the geography of Cuba's plant life, not to detail it.

## II. GEOGRAPHY

Cuba (Fig. 2) holds a unique position among the islands of the Antillean Archipelago. Of all the West Indies, it is the largest, the farthest west, and with the exception of the small and scattered Bahama Islands, it is the farthest north and nearest to the North American Continent.

The island lies between the  $20^{\circ}$  and the  $23^{\circ}$  parallels of north latitude, extending slightly beyond each, and between the  $74^{\circ}$  and  $85^{\circ}$  meridians of west longitude. The  $80^{\circ}$  meridian and the  $22^{\circ}$  parallel cross near the center of the island.

Cuba is usually described as crescentic in outline with its concavity to the south-west. This is only superficially true. Ignoring the southern dip of the western end, the topographic axis of the island extends directly west north-west.

The outline of Cuba, as it now exists with its many outlying cays, is due to a recent submergence which converted low elevations of the mainland into cays. The eight-fathom line gives a truer picture of the general form of the island (Fig. 3). Emergence to this line would increase the area of Cuba by 30 percent, and leave it surrounded by deep water.

Cuba is 720 miles long, and averages about 50 miles in breadth with a maximum of 120 and a minimum of 22 miles. The area is 43,000 square miles, to which at least another 2,000 should be added to include hundreds of islets and keys, and the Isle of Pines. There are 2,500 miles of coast. Much of this is swamp, but the coast is very varied in formation, changing so often from wooded slope to granitic cliff, coral rock, alluvial plain, sandy beach, and swamp that frequently all are met within a few miles. The southern coast of Oriente attains the greatest altitudes. Between Cape Maisi and Santiago de Cuba the escarpments reach a sheer 600 feet. West of Santiago the coastal land is at its maximum height, for here rests Pico Turquino, its summit 6,580 feet above the sea.

The coast of Cuba is remarkable for its numerous and excellent harbors. On the north shore, from west to east, there are Bahia Honda, Habana, Matanzas, Cardenas, Nuevitas, and Nipe; and on the south shore, from east to west, are Guantanamo, Santiago de Cuba, and Cienfuegos, all first-class harbors, several deep enough to receive "ships of the line." There are, in addition, numerous good anchorages, which include Cabanas, Sagua la Grande, and Baracoa on the north, and Manzanillo, Santa Cruz, Batabano, and Trinidad on the south. The pouch shape of many of the harbors gives them excellent protection from storm and attack. Small bays suitable for coastal traffic are innumerable.

Extending the greater part of the length of the island, with one interruption, is a central plain rising to an average elevation of 220 feet (Fig. 4). It is remarkably level and except for one major interruption is continuous from one end of Cuba to the other. In the west, this plain is the agricultural land and in the east the grazing land of Cuba.

The mountains of Cuba are in five widely separated groups, the largest of which occupies the entire eastern end of the island. At the western end, in Pinar del Rio Province, are numerous parallel ridges usually grouped as the Cordillera de los Organos, though sometimes distinguished as separate ranges. They are, however, one geological unit.

The mountains in Santa Clara Province of central Cuba are in three groups, northern, central, and southern. Several low ranges a few hundred feet high make up the northern mountains: Sierra de Bamburanao, Sierra de Meneses, Sierra de Jatibonico and Sierra de Matahambre. In the central group are Sierras de Agabama, Escambray and Rodriguez. The Lomas de Trinidad and their southeastern extension, Sierra de Sabeti Spiritus, are the southern mountains. Pico Potrerillo (3,602 ft.) and Pico Tetas (3,335 ft.) are in the former.

In east-central Cuba, or Camagüey Province, are the low Sierra de las Cubitas, 30 miles long and not more than several hundred feet high.

In Oriente Province are the island's greatest mountains. Just west of Santiago, paralleling the southern coast, are the Sierra Maestra containing Pico Turquino, Cuba's highest summit, with an altitude variously estimated between 6,500 and 7,500 feet. The writer has chosen 6,580 feet as the most likely height of Turquino. The central and northern Oriente mountains are geologically distinct from the coastal Sierra. They include the Sierra de Nipe rising to 3,790 feet, the Sierra de Cristal with a 4,300-foot peak, the Cuchillas de Tour, the Sierra de Purial with 4,020 feet to their credit, Sierra de Moa, Sierra de Frijol, and Sierra de Baracoa or Laguna-Baracoa.

The last is a group in which we shall have an especial interest. It rises from the easternmost shore of Cuba.

Politically, Cuba is divided into six provinces, which are, from east to west, Oriente (Santiago), Camagüey (Puerto Principe), Santa Clara, Matanzas, Habana, and Pinar del Rio. Topographically, the island consists of five natural divisions; from east to west these are mountainous Oriente, the savanas of Camagüey, the hills of Santa Clara, the flat, arable plain of western Santa Clara, Matanzas, and Habana Provinces, and southern Pinar del Rio, and the broken country of northern Pinar del Rio.

Cuban towns are many, though but few attain large size. The major ones suggest prosperity, and two, the capital, Habana, and Cienfuegos, the "Pearl of the South," have a tone of elegance. Camagüey is the principal town of central Cuba. Santiago de Cuba, capital of Oriente, is the chief city of the east, and the second largest town and port of Cuba. The city of Pinar del Rio is the capital of Cuba's western province, and ranks fifth in size. On the south-central coast is ancient Trinidad, and on the north-central coast, more modern Cardenas and Matanzas. Among the smaller towns, Baracoa on the northeastern shore is Cuba's oldest, Santiago and Trinidad being next in age. The population of Habana is 543,000, of Santiago 104,000, of Camagüey 130,000, and of Pinar del Rio 63,000.

### III. GEOLOGY

According to R. H. Palmer, in an as yet unpublished outline of the geology of Cuba, based on a paper presented before the Eighth American Science Congress, 1940, Cuba may be divided into eight physiographic provinces:

1. The Organos Mountains in the northern half of Pinar del Rio Province. This range is of hard Cretaceous limestone overlying younger shales and sandstone in an overthrust position. Erosion has dissected the limestone sheet into large isolated blocks called "mogotes" (Fig. 16). The flora of the mo-



FIG. 3. Outline of Cuba with eight-fathom line.

gotes is distinctive and abundant in spite of a dearth of soil.

2. The Cayetano Plain. This is a small area between the Organos Mountains and the north coast in western Pinar del Rio Province. Vegetation is scant.

3. A folded zone in the northern half of Habana Province. Erosion has removed the Tertiary limestone in part and exposed softer Cretaceous shales, leaving low rolling hills flanked on either side by the Tertiary limestone cliffs. The soil derived from the Cretaceous is considered mediocre in Cuba. Cane is the principal crop.

4. The Western Coastal Plain. This extensive central plain characterizes Cuba more than any other geological feature, at least to the casual visitor. It extends from Pinar del Rio, south of the Organos Mountains, eastward to Cienfuegos. In western Matanzas the plain crosses the island to the north coast. It is, in the main, of red soil, with much underground drainage. Where the soil is fairly deep it produces the finest cane land in Cuba. Where rock is near the surface, the porous limestone drains so thoroughly that desert conditions and a xerophytic flora prevail.

5. Santa Clara Province forms a single but complicated physiographic unit. In the north, low ridges form a Cordillera. In the center, low hills of igneous rock prevail. In the south, are the Trinidad Mountains with peaks nearly 3,000 feet high.

6. The Eastern Coastal Plain. This plain occupies the southern half of Camagüey Province and extends eastward across the Cauto Valley to the Sierra Maestra in Oriente Province. In practically all respects this Eastern Coastal Plain is identical to the Western one. Soil and agriculture are the same. The two may be regarded as one plain, interrupted by the Santa Clara overthrust and intruded zone.

## 7. The folded and intruded area in northeastern Camagüey and Oriente Provinces.

## 8. The Sierra Maestra of southern Oriente, and the mountains of eastern Oriente.

Without attempting a detailed account of the geological column in Cuba such as Palmer has so excellently given, attention is called to a few salient features which determine some special characteristics of Cuba's vegetation. One of these, the limestone mogotes in Pinar del Rio, has been mentioned.

Bordering the coast in many places is a narrow collar of hard limestone much of which is badly eroded producing dog-toothed calcareous rock, and some of which is cut into terraces on one of which Morro Castle rests. The highest of these terraces are in eastern Cuba, at Maisi.

Another and quite other geological feature determining vegetation are the igneous outeroppings. There was much igneous activity in Cuba during the upper Cretaceous. The resulting deposits are tuffs and flows that erosion has exposed in broad bands in every province. The igneous rocks are both intrusive and extrusive, both acid and basic. The basic rocks are for the most part serpentine of a later age. There are serpentine intrusions in the Organos Mountains, the Habana-Matanzas anticline, the Santa Clara over-thrust, central Camagüey, and some disturbed areas in Oriente Province. The central Camagüey serpentine harbors a very distinctive vegetation to which considerable attention will be devoted. These soils are among the poorest agricultural grounds in Cuba, and in general support a very scant natural plant growth characterized particularly by palms such as *Sabal parviflora*, *Coccothrinax miraguano*, and *Copernicia macroglossa*.

Serpentine rich in iron supports good pine forests. On these soils in western Pinar del Rio grow *Pinus caribaea* and *P. tropicalis*. On igneous ridges in the Sierra Maestra of southeastern Cuba the pine reappears.

Of volcanic activity there has been very little in Cuba since the Cretaceous, the thick Eocene basaltic series of the Sierra Maestra being the only exception.

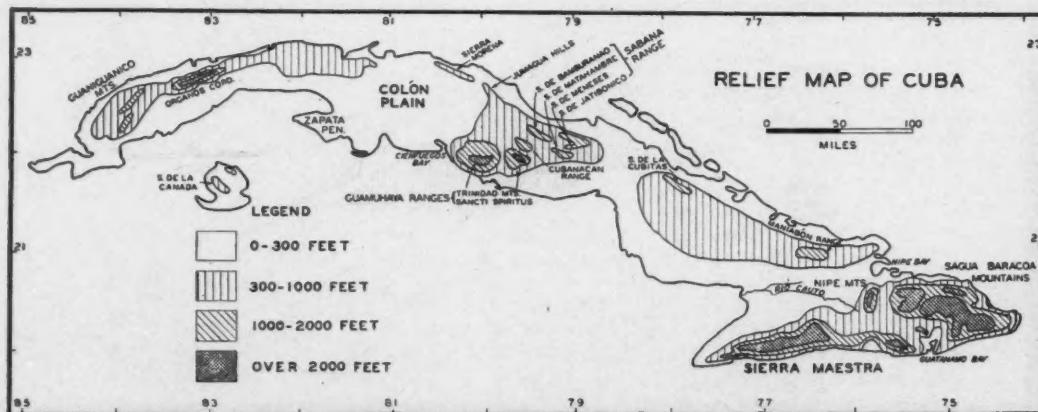


FIG. 4. Relief map of Cuba (from T. W. Chamberlin, *Weather Review*, 68: 4, 1940).

## IV. CLIMATE

## 1. TEMPERATURE

The climate of Cuba is a very equitable one. Though the island lies wholly south of the Tropic of Cancer, it is near enough to the temperate belt to have a relatively moderate temperature the year round. The summers may be hot at times but they rarely have the excessively high temperatures of some northern cities; 90° F is not often exceeded; 80° F is the average maximum on the coast. The winters are cool but not often cold; 40° is rare, 50° infrequent, 60° common, and 68° the mean minimum temperature from November to March. Ice is never formed in Cuba, at least, so says the official record, but during the winter of 1939-40, one of the coldest known in Cuba, there were reports of freezing temperatures at several localities. None of these, however, was authentic, yet from a reliable source the writer has the statement that frost was formed in Central Trinidad in 1932. If this is true, then freezing temperatures on the summits of Cuba's highest mountains must occasionally occur.

The mean monthly temperatures and the mean maxima and minima for the seacoast, at Habana, are (in degrees F):

Jan.	Feb.	Mar.	Apr.	May	June	
70.6	70.8	72.9	75.1	77.5	79.2	
Max.	73.4	75.0	76.1	78.8	80.2	81.1
Min.	66.9	68.2	68.9	72.1	75.0	77.9
July	Aug.	Sept.	Oct.	Nov.	Dec.	Annual
80.1	80.3	79.8	77.8	74.3	71.9	75.9
Max.	82.8	82.9	82.0	80.4	78.1	74.1
Min.	78.4	78.4	77.7	75.9	71.1	68.0
						74.5

It is thus evident that Cuba has an ideal tropical temperature, never exceedingly hot and always free of extreme fluctuations. This is not only true of Habana, but of the entire island. Among ten stations, from Pinar del Rio to Santiago, there is only 7.6° difference between the highest and lowest normal monthly temperatures for January, and but 5° difference between the highest and lowest normals for August.

The uniformity of the temperature of the island as a whole is further shown by comparisons of annual temperatures. Santiago, with a normal annual temperature of 78.8°, is the hottest place in Cuba, but it is only 5.5° above Camajuani, the coldest station on the island with a normal annual temperature of 73.3° F. The normal annual temperature of Pinar del Rio at the western end of the island is but 1.2° below that of Santiago at the eastern end. The foregoing refers to the lowlands of Cuba. At the highest altitudes lower temperatures are reached.

Except for mountain summits, plant distribution in Cuba is little influenced by temperature. Rainfall and soil determine the natural vegetation.

## 2. MOISTURE

Unlike temperature, the rainfall of Cuba differs greatly between parts of the island (Fig. 5). The monthly variation at any one station is very great (Fig. 6). Differences in monthly, seasonal, and yearly precipitation are likewise pronounced. The total annual rainfall for one year may be double that of another year in the same locality; thus, at Pinar del Rio in 1907, 39.8 inches of rain fell, and in 1909, 84.7 inches.

Differences in annual precipitation may be very great at nearby stations. It is only 18 miles from Matanzas to Union, yet the yearly rainfall at the former town is 52 inches and at the latter 71. Particularly extraordinary here is the fact that the intervening country is flat, with no topographic feature upon which to base an interpretation of the differences in precipitation. Still greater is the difference in rainfall between Habana, with an annual precipitation of 43 inches, and Batabano in the same province with 65 inches; the one is on the north coast and the other on the south coast, but there are no intervening mountains.

One is likely to hear that the vegetation of the wet eastern end of Cuba contrasts most sharply with that of the dry western end. The writer's several sojourns on the island corroborate this, but the rain

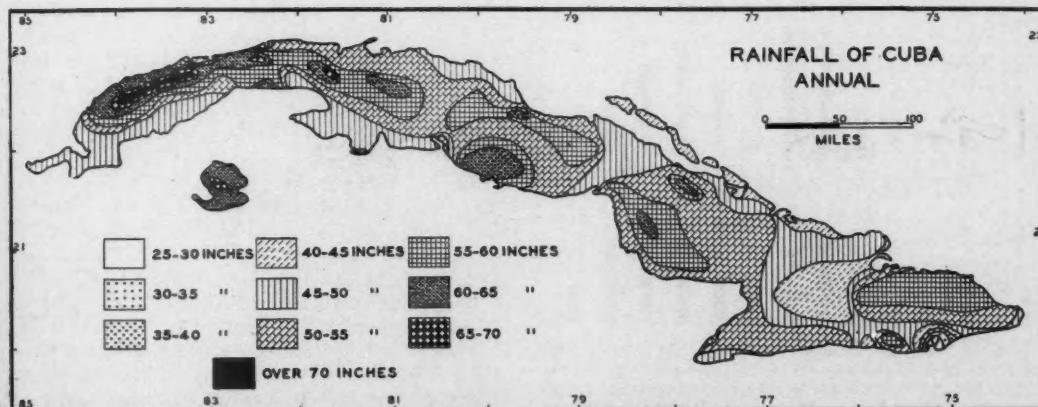


FIG. 5. Rainfall map of Cuba (from O. L. Fassig, Tropical Plant Res. Foundation).

charts (Fig. 5) contradict it. The total annual precipitation of humid Oriente is 46 inches whereas that of "dry" Pinar del Rio is 63 inches; and the

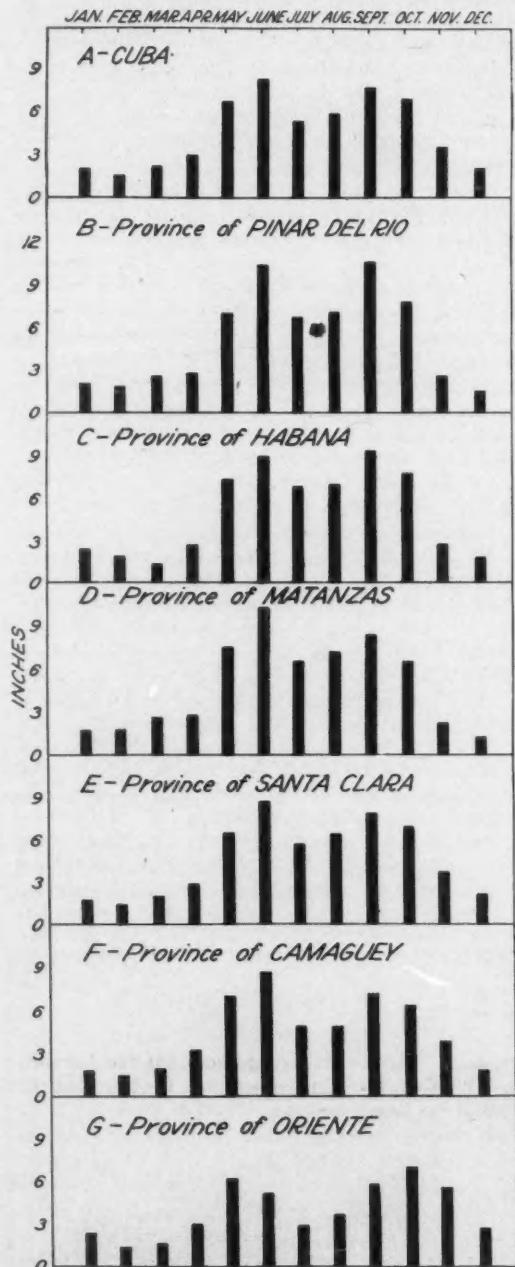


FIG. 6. Average monthly rainfall in Cuba from 1899 to 1924, based upon records in 19 localities. A. for the entire Island; B-G for the Provinces: expressed in inches and hundredths of an inch (from O. L. Fassig, *Tropical Plant Res. Foundation*).

annual maximum of Pinar del Rio over a period of 25 years is 89 inches whereas the annual maximum for Oriente is 62 inches. Fig. 6 shows Oriente to be actually drier than Pinar del Rio. The apparent contradiction rests, first on the fact that the total rainfall of all Oriente is misleading, it tells nothing of the diversity in local rainfall. The official rainfall data do not, unfortunately, include either of the localities where the maximum and minimum precipitation of Oriente Province occur. The north coast is wet, the south coast dry, and the eastern Cape Maisi very dry. Then there is the significant factor of moisture retention, which is in great measure a soil quality, but also atmospheric, both topography and vegetation affecting it. The very vegetation which the higher humidity makes possible is in its turn a factor in maintaining high humidity.

It is not always an easy task to interpret rainfall distribution. In addition to the factors so far mentioned, prevailing winds are of prime importance, but even with their help one is often left without an adequate explanation. Where the distribution of rain is determined by an obvious topographic feature, analysis of the situation is easy. This is true in Jamaica where a 7,000- to 9,000-foot ridge extends the length of the island on an east-west line and intercepts all clouds coming from the northeast. These water-laden clouds carried by the trade winds at 2,000 to 5,000 feet altitude, strike the northern mountain slopes and deposit their moisture. What few roll over the high ridge are quickly dispersed by the hot dry air rising from the southern valleys. The result is a wet north coast with luxuriant vegetation, and a dry south coast sparsely covered by xerophytes.

The situation in Cuba is not so easy of analysis, for the mountains are lower and more scattered. It is, however, possible to make some general statements. Running parallel to the southeastern coast of Cuba are the Sierra Maestra, sufficiently high (6,000 feet) to halt clouds carried by trade winds which keep the northern slopes of the Maestra wet and leave the southern slopes comparatively dry. Cacti, agaves, Plumeria, and other xerophytic plants are scattered along the southern coast from Santiago westward to Cape Cruz. The extraordinary dryness of Cape Maisi is due, as in the case of the Bahama Islands, to the absence of mountains. There is no barrier in the direct line of the trade winds, so the moisture-laden clouds pass by.

This is as far as one can go in the way of a direct topographical interpretation of the distribution of precipitation in Cuba, but there are other factors which come into play in a secondary way, exerting considerable influence. Run-off and porosity of the ground are often responsible for aridity in regions where rainfall is ample. In this way is the presence of a rich plant life at Baracoa and a xerophytic vegetation on the Hicacos Peninsula to be explained, though both are on the north coast of Cuba and both receive the same annual precipitation

—Baracoa 45 inches, and the Hicacos Peninsula 46 inches. At Baracoa there are abundant marls which retain moisture. The Hicacos Peninsula has a soil of loose sand through which water runs as through a sieve.

The desert plain at Maisi on the eastern end of Cuba presents a similar situation. It is a recently elevated series of limestone ledges with little soil to retain precipitation and many crevices to lead it away. It gets little rain to start with and the run-off is nearly 100 percent. The country surrounding Matanzas is another example. One side of the bay is a series of recently elevated limestone reefs the vegetation of which is xerophytic. A few kilometers away are cultivated farms on Cretaceous marls and shales, which, exposed by erosion, hold water well. Still another factor which makes for aridity in a coastal area with ample rainfall is salinity of the permanent subterranean water.

The foregoing interpretation of arid areas in regions of abundant rain has had to do with coastal land where recently elevated porous coral reefs are common, but there are inland examples of the same situation. These are the mogotes or limestone hillocks which occur in Habana and Pinar del Rio Provinces (Fig. 18). The mean annual average rainfall of the latter Province exceeds that of any other, yet the mogotes there are dry. This again is true because weathered limestone hillocks have little soil in which to hold water, and their precipitous slopes with many fissures lead it away. The mogote harbors a distinctive and thoroughly xerophytic vegetation.

#### V. PLANT AFFINITIES BETWEEN CUBA AND NEIGHBORING COUNTRIES AND THE CAUSES THEREOF

The origin of an island's flora presents an interesting problem. The Cuban situation is especially unique because the island lies near both Florida and Yucatan, 140 and 125 miles, respectively, yet its flora is primarily South American from which continent it is separated by 600 miles of water. If one had only a map by which to judge, one would say that the fauna and flora of the Greater Antilles are principally Central American with strong affinities to North America and a feeble relationship to South America. But quite the reverse is true, for the plant life of Cuba shows great similarity to that of South America, less to Central, and little to North America.

Plant distribution involves two primary factors, dispersal and establishment. Dispersal may be by wind, ocean currents, or animals. But it is not enough for a plant to be transferred to new country. It must become established once it has arrived, the new habitat must be suitable.

Where plant affinities exist between countries separated by large bodies of water, and ordinary means of dispersal seem inadequate, it was once customary to assume the presence of a former land bridge.

The building of land bridges has been rather overdone, yet there is geological evidence enough to indicate that the earth's surface has changed through the ages. Such changes have been frequent in the Caribbean area, ample to explain some features of plant affinities existing there. There is also much justification for reversing the line of reasoning and seeing in the close relationships between plants on separated land areas support of geological evidence that the past configuration of the earth's surface differed from that of today.

There are many ways in which plants could be, and undoubtedly have been, distributed over the earth's surface. As land connections are but one of them, plant affinities between distant lands are not necessarily an indication of former bridges. However, there are situations where plant relationships and distribution are such as to give very convincing evidence of former land connections. Such is the case among the Pacific islands where the distribution of many plants is such as to produce a sharp boundary line that winds among the islands in a way inexplicable on the basis of wind, bird, or similar means of dispersal, but it is quite understandable when the islands to the west of the boundary line are regarded as remnants of a former single land mass.

There are four routes by which plants may have reached Cuba, namely, via Yucatan, Florida, the Lesser Antilles, or directly over water from Venezuela. The first three of these routes might have been by land bridges. The journey by way of the Lesser Antilles is a shorter water route than usually appreciated, for the widest gap is only 90 miles. Urban believed that the plants of Cuba and Hispaniola came from South America by way of a continuous land connection formed by the Antilles. The objection to this hypothesis lies in the fact that the Lesser Antilles are volcanic, and of later origin than the Greater Antilles. Geological evidence is in opposition to an Antillean bridge in recent epochs. It does not, however, preclude land connections in earlier eras, for granite lies beneath the lava surface of the Lesser Antilles. The mountains under the sea which form the West Indies are an extension of the Central Andean Cordillera and connect with the Mexican Highland through structures in southern Yucatan. But Urban's suggestion that the Leeward and Windward Islands rather than Central America formed the bridge by means of which plants migrated from South America to Cuba must be rejected for other reasons. The granitic substratum which indicates continuity in land structure was repeatedly submerged before the present flora was established. That this is true is indicated by genera common to Venezuela, Colombia, and the eastern United States without a single representative in Middle America. It is possible that a former land mass, in its submergence, carried with it all Antillean representatives of these genera.

Geologists once postulated a land mass in the place of the present Caribbean Sea and called it "Antillea." Belief in it has waned. Even so short a bridge as that between Cuba and Florida is questioned because of the Straits of Florida; the trough is 4,000 feet deep. But no land bridge is needed to explain the presence of plants common to Cuba and Florida, for the water passage is short; winds, birds, and drift wood are sufficient.

In opposition to the foregoing evidence in support of land bridges is the fact that plants do not always use a land connection when it is present. Proof of this lies in the dissimilarity between the mountain floras of the eastern and western United States though the great plains have long served as a bridge. Almost the same situation pertains to Cuba and Yucatan, for in spite of a possible former land mass joining these two countries, the dissimilarity in the floras of the two regions is greater than the affinities.

Still another fact in opposition is the quite obvious lack of land bridges in regions such as Polynesia where plant relationships exist between far distant bodies of land. Thus, Hawaii is 2,000 miles from North America, and over twice as far from any large land area in other directions. There is little probability of a land bridge in any direction, yet the relationship of the Hawaiian flora is predominantly with that of the Indo-Malayan-Melanesian region, and scarcely any with America which is but half as far away.

Land bridges have undoubtedly played a significant role in plant distribution, but other means of migration, such as wind, migrating birds, ocean currents, and natural rafts, have probably had as great a part. Wind currents of hurricane force would carry small seeds for many miles. The feathered coats of migratory birds, and mud on the feet of aquatic birds are sufficient to account for the distribution of plants over distances as great as that separating Canada and the Andes. The intestinal tracts of birds will bring about seed dispersal over shorter distances.

Among other means involved in plant and animal migration, natural rafts have certainly played a prominent role, probably greater than ordinarily appreciated.

All of the foregoing means have most likely contributed to the introduction of plant life into Cuba.

The foregoing discussion on means of plant migration has had to do with the ways in which plant affinities between Cuba and neighboring countries have been established. Evidence that these affinities exist will now be presented.

On entering Pinar del Rio Province a North American is immediately impressed by the presence of pine and oak. These two genera are not uncommon in the tropics the world over. Both occur in Hispaniola and Central America, pine is in the Philippines and oak in Java. Yet, neither genera is typical of the tropics; their presence there suggests migration from the north.

The Cuban oak is *Quercus virginiana*, the same

that inhabits the southeastern United States, as far north as New Jersey. The pines of Cuba are of several species, both *P. tropicalis* and *P. caribaea* being common, the latter is abundant in Florida. Oak and pine, common to Cuba and the United States, are among the strongest plant affinities occurring between the two countries.

Southern Florida and the Keys have a prolific growth of the legume tree-shrub, *Lysiloma bahamensis*, which is characteristic of all thickets in tropical America. Among the woody legumes common to warm and arid coastal lands in the Americas, there are, in addition to *Lysiloma bahamensis*, *Pithecellobium unguis-cati*, *P. guadalupense*, *Neptunia floridana*, *Cassia ligustrina*, *C. bahamensis*, *Caesalpinia pauciflora*, *C. ovalifolia*, *Guilandina crista*, and *G. bonduc*. If to these are added other plants common to the southeastern United States such as *Guaiacum sanctum*, *Byrsonima cuneata*, *Zanthoxylum fagara*, *Z. coriaceum*, *Amrys elemifera*, *A. balsamifera*, *Pieramia pentandra*, and *Bursera simaruba*, a list of plants typical of the arid, lowland thickets of Cuba is obtained.

Still another plant abundant in Cuba and Florida which gives additional indication of plant relationships between the two countries, is the royal palm, *Roystonea*. Equally significant too are the affinities between Cuban and Floridian ferns. Those of Florida are limited to the calcareous hills north of Tampa, thus finding habitats similar to the limestone of Cuba's mogotes.

Not all plants common to the Antilles and to North America are of distributional significance; such are strand plants in general, and in particular, *Sambucus canadensis*, *Cephaelanthus occidentalis*, *Typha angustifolia*, *Pontederia cordata*, *Sagittaria*, *Nuphar*, and *Nymphaea*.

In conclusion it may, therefore, be said that though the major portion of Cuba's plant life came from the south, there are some strong ties with the vegetation of southern North America. Whether these plants came via Florida or by way of Mexico is not known.

The situation pertaining to plant affinities between Cuba and Mexico, especially Yucatan, is still less well understood than that between Cuba and Florida. Affinities there are. One authority finds a Cuba-Yucatan-Oaxaca-Vera Cruz-Texas-Florida distribution for a number of species, thus linking Cuba with both Central and North America. Other authorities, on the other hand, say that in identifying unknown West Indian plants look first to South America. The nearness of Cuba to Yucatan is sufficient reason to expect strong plant ties between them. This is suggested by the following species common to Cuba and Yucatan: *Caesalpinia violacea*, *Atelis cubensis*, *Pithecellobium keyense*, *Ficus laevigata*, *Brosimum alicastrum*, *Metopium brownei*, and *Eugenia fadyenii*.

The evidence indicating a Venezuelan and Colombian ancestry of Cuban plants is strong and is indicated by many species common to the two lands;

among these, the following are outstanding: *Costus spiralis*, *Vitex divaricata*, *Clerodendrum indicum*, *Citharexylum spinosum*, *Sacoglottis amazonica*, and *Morinda major*.

## VI. THE PLANT ASSOCIATIONS OF CUBA

### 1. COAST

#### A. STRAND

To place foot again on a tropical sandy shore with its coconut palms bending seaward is a glorious experience. A plant geographer will wander along the water's edge seeking plants with which he is familiar, hoping also for an endemic or two.

It is a general phytogeographical rule that arctic plants are circumpolar, with an ever-decreasing number of around-the-world species as one goes southward, but there are some few tropical plants which follow the equator through both hemispheres; this is true of the beach morning-glory (*Ipomoea pes-caprae*) as typical of the shores of the Caribbean as those of India.

On approaching a tropical American coast the coconut is likely to be the first plant seen because of its size and frequent occurrence, but it is Old World in origin and so not American. One might select the mangrove (*Rhizophora mangle*) as the plant most characteristic of American coasts. It certainly is abundant, and very typical of Cuba. But the genus is pan-tropic, and the species on West African shores, particularly in view of the fact that the vegetation of the coast is in large measure dependent upon the seagrape. *Coccoloba uvifera* grows near the water, fringing the shore, and forming a natural break against severe winds which few plants can withstand. Seaward of the *Coccoloba* hedge grow mostly low succulent herbs and grasses. Landward are woody tree-shrubs.

The strand vegetation starts near the water's edge where the world-wide beach morning-glory is found. Exceedingly long stolons permit it to get near the sea, though basal portions are well grounded quite some distance back from the sea.

A frequent companion of the beach morning-glory is the legume, *Canavalia maritima*. Both have the habit common to psammophytes, that of putting out roots at every node along the runner. *Ipomoea*, a morning-glory, and *Canavalia*, a legume, are readily distinguished when not in flower by their leaves, that of *Ipomoea* is cleft, whence its other common name, the goat's foot morning-glory. Farther inland climbing on shrubs and trees, is another *Canavalia*, *C. nitida*.

Typical of every strand are the psammophytic grasses. In Cuba their number is great, with *Uniola paniculata* and *Sporobolus* species predominating.

Succulents particularly characterize the sandy shores of Cuba. They grow at the inner edge of the strand where sand merges with clay. The most

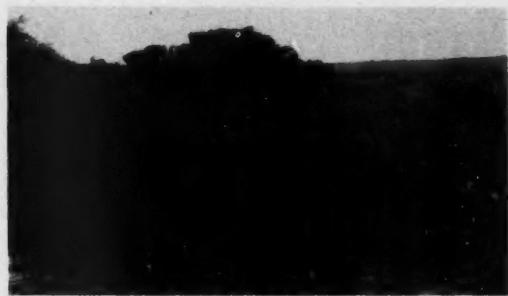


FIG. 7. *Turnefortia gnaphalodes* on the sandy shores of Cuba.

abundant of these are *Turnefortia gnaphalodes*, *Suaeda linearis*, *Suriana maritima*, *Borrichia arborescens*, and *Strumpfia maritima*. Though all are widespread on Cuba's coast, *Turnefortia* is deserving of special mention (Fig. 7). It is the incienso de playa of the Spanish, notable not only for its pungent odor, but even more so for its decorative value. It is a picturesque plant, of a soft, mouse-grey color. Its value as an ornamental is beginning to be appreciated by tropical gardeners. There are numerous species in Cuba, including *T. gnaphalodes*, *T. peruviana*, *T. bicolor*, and *T. syringaeifolia*, the last a vine.

Coastal dunes are not numerous in Cuba, but when they occur the dominant strand psammophytes take possession of them.

The inner boundary of the strand association is marked by *Coccoloba uvifera* (Fig. 8).

The seagrape hedge which fringes the sea is not of one plant, it is a plant association. It is not an integral part of either the vegetation between it and the sea, nor of the vegetation back of it, whether thicket, savana, or desert. The hedge is itself a community of plants in which the seagrape is dominant (Fig. 55).

The associates of the seagrape in this elongated plant community which borders the sea vary with the locality. Common among them on all Caribbean shores is *Chrysobalanus icaco*, the hieaco or coco-plum. It is rarely over 15 feet high. Occasionally, too, the toxic manzanilla *Hippomane mancinella*, is there. In more favorable habitats it grows into a large tree. Another frequent inhabitant of the seagrape hedge is the toxic *Comocladia dentata* (Fig. 38), widely distributed but always in arid localities. Somewhat different is the composition of the seagrape hedge at Maisi, under which heading it will be presented. Among the plants which compose the narrow strip of vegetation that borders the sea only the seagrape is wholly restricted to it.

#### B. ROCK

Much of Cuba's coast is rock. Some of it is low and some rises to precipitous heights directly above the sea, often forming mammoth terraces, each with its own distinctive flora. On the low coastal rocks

FIG. 8. Leaves and fruits of *Coccocoba uvifera*.

of Cuba grows a most picturesque plant guild. It is well developed at Varadero on the Hicacos Peninsula and on occasional untouched ground near Havana and westward. Here are two wholly unlike ecological types, yet each in its own way fully adjusted to an arid habitat. The community—it is the same wherever found on Cuba's northwestern coast—is dominated by four plants, growing on eroded calcareous rock. Two are diminutive succulents, with globular purple leaves, *Trianthema portulacastrum* and *Philoxerus vermicularis*; and two are procumbent woody shrubs, *Conocarpus erecta*, which is prostrate here but erect on good soil, and the minutely leaved *Rhachicallis americana*. *Rhachicallis* reaches 2 feet on sandy ground, but becomes more and more depressed the closer it is to the sea, until near the water's edge it lies flat to the rocks.

The similarity between this coastal rock association and an alpine flora is striking. The thick-leaved succulents, *Philoxerus* and *Trianthema*, have their counterparts in the alpine *Sedums* and *Sempervivums*, all members of the Crassulaceae. And the prostrate woody *Conocarpus* is an exact facsimile of the procumbent alpine willows. All show adaptations to a rocky, or alpine, habitat. The thick leaves of the Crassulaceae, the low-lying gnarled forms of the woody plants, and the minute leaves of *Rhachicallis* are typical adjustments to an arid environment. Though their altitudes differ by 6,000 feet or more, the surroundings of alpine crags and rockbound

coasts are similar, windswept, soilless, and dry. The vegetation of extensive coral shores and calcareous rocky cliffs will be treated under other headings.

#### C. SWAMP

Few Caribbean shores are without their swamps, but Cuba has inherited more than her share. Mile upon mile of mangrove entanglements line her coast (Fig. 9). The largest mangrove swamp in Cuba, if not in all the American tropics, is that of the Zapata Peninsula on the southern shore. It covers some 500 square miles.

The most prolific of the mangroves is *Rhizophora mangle*, called in Cuba mangle colorado or the red mangrove. It is the common mangrove throughout the tropics of the Americas and West Africa. In the Orient it is replaced by *R. mucronata*. There are at least four other genera commonly called mangrove in the American tropics; indeed, there are even "mountain mangroves," though not in Cuba—this name applies to species of *Tovomita* in Dominica and to *Clusia* in Trinidad. The five Cuban mangroves are *Rhizophora mangle*; *Picroidendron macrocarpum* called mangle negro; *Laguncularia racemosa* called mangle bobo or white mangrove though better known as pataban; *Conocarpus erecta* called mangle boton, and *Avicennia nitida* called mangle prieto. Aside from their taxonomic differences they are also sharply distinguished from one another by their geographic distribution. *Rhizophora mangle* is best able to withstand the onslaught of the waves. It alone puts out to sea with success. Farthest inland, in brackish swamps, or up river estuaries where salt water mixes with fresh, grows *Conocarpus erecta*. Midway occur the three others.

The distribution of mangroves from the open coast inland is determined by a number of factors. A tight grip on the loose soil under water is necessary to survive in the face of the open sea, and *Rhizophora mangle* is able to accomplish this best, because, among all mangroves, none has so excellent a development of arching stilt roots. *Rhizophora* forms impenetrable thickets along many miles of Cuba's coast against which a lashing sea makes little impression (Fig. 10). Tolerance of salt is next in importance in determining distribution. *Rhizophora* tolerates high salinity best, and *Conocarpus* endures it least well.

It has just been stated that the ability to endure concentrated salt water by *Rhizophora mangle* permits it to put farther out to sea, thus assuming



FIG. 9. Mangrove swamp.

FIG. 10. *Rhizophora mangle*.

that it is a matter of tolerance rather than preference; yet most mangroves, *Conocarpus* being an exception, are associated with brackish water.

Coastal swamps in Cuba, whether containing mangroves or not, are likely to harbor the following semi-aquatic plants: *Cyperus bruneus*, *Distichlis spicata*, *Dalbergia ecastophyllum*, *Rhabdadenia paludosa*, *Batis maritima*, and the fine, tall swamp ferns *Acrostichum aureum* and *A. danaeifolium*.

## 2. DESERT

The deserts of Caribbean shores are magnificent examples of a most uninviting yet fascinating tropical vegetation. The ecologist will find them nothing short of inspiring. The heat is intense, the light blinding, every plant armed, no water, no shade, no trail leading anywhere; as awe-inspiring, as fearful, as superb a picture of the eternal persistence of life under the most adverse conditions that Nature can produce.

When first the writer used the word desert in reference to arid regions in Cuba, his colleagues there questioned its applicability to the dry shores of the American tropics. To them, deserts are such as the great Sahara, the like of which, regardless of size, Cuba does not possess. It is true that there is nothing in the American tropics comparable to the Sahara or other great deserts of the Old World, but deserts may be defined in terms of vegetation, kind of vegetation, or sparsity of species. If a desert must be of sand, must possess shifting dunes, then the coast of New Jersey, or the shores of Lake Michigan are more desert than any Caribbean land. If a desert is arid waste land covered with an open xerophytic vegetation, then certain areas in Arizona and New Mexico, and many on Caribbean shores are as much desert as the Sahara.

Semi-desert is often applied to the dry regions of the American tropics, but these areas are not semi-anything. If soil is the criterion, arid Caribbean

coasts are not deserts in the Old-World sense at all. If moisture and plant life are the criteria, the dry coasts of the Antilles are thoroughly desert.

Caribbean deserts, common with deserts the world over, consist of three ecological plant types, hard-wooded and usually microphyllous thorny shrubs, persistent succulent plants, and ephemeral herbs. The sclerophyllous shrubs on American deserts are most often legumes; they are species of *Acacia*, *Mimosa*, *Pithecellobium*, and *Prosopis*. The succulents are principally cacti, species of *Opuntia* and arborescent relatives of the genus *Cereus*. The ephemeral herbs are escapes from adjoining ground.

The finest desert on any Caribbean coast is at Gonavales, Haiti. Cuba's best is at Maisi (Fig. 57). Cacti and microphyllous shrubs are the dominants. Among the cacti, the colossal arborescent *Dendrocereus nudiflorus* (Figs. 11, 61) is very striking. That its mammoth trunk is the stem of a cactus one hesitates at first glance to admit. The columnar *Lemairocereus hystrix* is an equally fine tall cactus (Fig. 11). *Cephalocereus brooksianus* appears at Maisi to be a dwarf form but actually it is kept low by the wind for it grows where the desert is wind-swept (Fig. 57). The most widely distributed of all Cuban cacti is *Opuntia dillenii*, which, oddly, is not abundant at Maisi, but its place is well taken by *O. macracantha*.

The prevailing legumes of Cuban deserts are species of *Acacia*, *Pithecellobium*, and *Caesalpinia*, with an occasional *Prosopis juliflora*. On the Maisi plain these occur as *A. spinosa*, *P. hystriz*, and *C. bahamensis*. More abundant is *Erythroxylon minutifolium*. Its very small leaves well adapt it to a xerophytic habitat (Fig. 12).

*Erythroxylon*, and its close relative, *Phyllostylon brasiliensis* (Fig. 59), called jatia in Cuba, are both microphyllous trees common on arid ground, whether desert or thicket. After all, desert and thicket may differ only in height and density of vegetation, the plants of the desert being dwarfed and sparsely scattered whereas those of the thicket are tall and compactly arranged.

FIG. 11. *Dendrocereus nudiflorus* in the center, *Lemairocereus hystrix* at the left.

I have frequently wondered at the extremes in plant types to be found in arid localities. They illustrate Nature's various ways of meeting the same situation, an answer to many ecological and biological problems. The desert vegetation of tropical America is characterized by two quite different kinds of plants; soft, thick-stemmed, succulent cacti, and hard-wooded tree-shrubs. Obviously, plants survive in arid climates either by storing water when it is to be had, or by storing none and reducing consumption and loss. The thick stems of cacti do the former, and the slow-growing, hard-wooded shrubs of deserts do the latter; their small leaves diminish transpiration to a minimum.

### 3. THICKET

There is no more common ecological type in the American tropics than the thicket. On certain West Indian islands, it exceeds all other plant associations. Some of the Lesser Antilles are all thicket. In Cuba, sabanas cover a greater area but thickets are numerous.



FIG. 12. *Erythroxylon minutifolium* ( $\frac{1}{2}$  life size).

The thicket is an ecological feature of all arid countries, whether tropical, temperate, arctic, or alpine. Its universal occurrence is indicated by the many names given to it. In southwestern America it is chaparral, in Brazil caatinga, in the Bahamas coppice, in France garrigue, in Spain jarales, and in Cuba manigua.

The naming of plant associations by their dominant plant is good practice, but difficult in the tropics where there are half a dozen dominants, which gives further support to the claim of Cuban botanists that a climax association in the sense of a pure stand is rare in the tropics.

The writer has considered the question of the most suitable word for Caribbean thicket and has ended by letting it remain at that. Schimper used several terms, of which "thorn-forest" and "thorn-woodland" were two, but thickets are not forests nor woodlands, as we usually visualize these. The most appropriate of Schimper's terms is "thorn-bush." However, thicket is a better expression for it brings to the American mind the same picture as coppice does to the Englishman, the picture of a closely packed, sun-baked association of low, woody, and often thorny tree-shrubs on arid land.

The vegetation of Caribbean thickets is xerophytic, such as is characteristic of dry, hot areas the world over. That aridity is a determining factor is obvious, yet the "dry" Hicacos Peninsula has 46 inches of rain a year, compared with 43 for New York and 22 for San Francisco and London. Precipitation is, therefore, ample. But aridity is, as already stated, also a matter of soil porosity.

Cuban thickets are mostly coastal (Fig. 13), though inland and alpine thickets are not uncommon in the Caribbean area. The coastal portion of thickets is primarily an expression of dry soil due to porosity and run-off. Still another determining factor is the wind. Not even the small and slender trees of thickets could withstand the wind were it not for that extraordinary and tenacious tree, the seagrape (Fig. 8).

I have already indicated the position of the seagrape (Fig. 13). It stands at the inner edge of the strand, paralleling the water line about 20 feet from it. Here sand merges into soil, which may be the secret of the seagrape's location, but more likely the well-defined habitat of the seagrape is due to lack of competition. It alone among large woody plants can withstand the whipping of the wind and sea. It is the most beaten and distorted plant of the American tropics, yet it survives with flourishing success.

From the procumbent succulents nearest the water's edge, there is a gradual increase in height of plants up to the top of the seagrape, and from there on inland there is a level canopy formed by the small trees and shrubs of the thicket (Fig. 13). This is one of the most interesting plant associations on Caribbean coasts.

The finest Cuban thicket, both in extent and profusion of growth, is that on the Hicacos Peninsula.

It may well serve as the prototype of all tropical American thickets. The Peninsula takes its name from the small hieaco tree (*Chrysobalanus icaco*), a common plant in Cuba and on Caribbean shores in general, yielding the coco-plum. But the hieaco does not dominate the plant life of the Peninsula. Guaya-canillo (*Guajacum sanctum*) is more abundant. The "little guayacan" is a close relative of guayacan, the lignum vitae (*G. officinale*). The guaya-canillo's magnificent crown of small blue flowers is of horticultural interest.

Neither of the two plants so far singled out as codominants of Cuba's coastal thicket is a legume, but Rosaceous (*Chrysobalanus*) and Zygophyllaceous (*Guaiacum*), yet it is the legumes which characterize xerophytic vegetation the world over. On the Hieacos Peninsula only *Caesalpinia vesicaria* is abundant. *Parkinsonia aculeata* and *Pithecellobium prehensile* fill out the rather meager list of legume trees for the Peninsula. Other arborescent legumes common in Cuban thickets, notably at Maisi, are *Phyllostylon brasiliensis*—it is a frequent member of the microphyllous guild on arid ground, in certain areas it dominates the thicket—and *Lysiloma latisiliqua*. The latter is a striking tree because of the remarkable habit of sloughing off its bark, outdoing in this respect the shagbark hickory of North America.

Two more plants may be singled out from the Hieacos thicket; one is the most abundant of Caribbean caeti, on desert and in thicket, *Opuntia dillenii*; the other is a palm, *Coccothrinax littoralis*, a Cuban endemic.

Plants common to Cuba's coast, on sand and rock, in thicket and swamp, are here listed in the order of their occurrence from the water's edge inland. Semi-aquatics are placed first because they are often at the edge of the sea, but equally often they are far inland, up river estuaries, or they may be wholly lacking. On non-swampy coasts the plant succession starts with *Ipomoea pes-caprae*, near the sea (as in Fig. 13).

<i>Rhizophora mangle</i>	<i>Trianthema portulacastrum</i>
<i>Avicennia nitida</i>	<i>Rachicallis americana</i>
<i>Picroidendron macrocarpum</i>	<i>Ipomoea pes-caprae</i>
<i>Laguncularia racemosa</i>	<i>Canavalia maritima</i>
<i>Conocarpus erecta</i>	<i>Ambrosia hispida</i>
<i>Philoxyerus vermicularis</i>	<i>Heliotropium curassavicum</i>

<i>Uniola paniculata</i>	<i>Casasia calophylla</i>
<i>Sporobolus indicus</i>	<i>Erihalis fruticosa</i>
<i>Suaeda linearis</i>	<i>Bidens pilosa</i>
<i>Suriana maritima</i>	<i>Euphorbia cassythoides</i>
<i>Borrichia arborescens</i>	<i>Iva imbricata</i>
<i>Tournefortia gnaphalodes</i>	<i>Passiflora cuprea</i>
<i>Coccobola uvifera</i>	<i>Guazuma tomentosa</i>
<i>Opuntia dillenii</i>	<i>Hypelate trifoliata</i>
<i>Plumeria alba</i>	<i>Solanum bahamense</i>
<i>Exostemma caribaeum</i>	<i>Citharexylum fruticosum</i>
<i>Caesalpinia vesicaria</i>	<i>Maba grisebachii</i>
<i>Guajacum sanctum</i>	<i>Bourreria revoluta</i>
<i>Coccothrinax littoralis</i>	<i>B. ovata</i>
<i>Jacaranda coerulescens</i>	<i>Lasiacis divaricata</i>
<i>Parkinsonia aculeata</i>	<i>Morinda roio</i>
<i>Tabebuia lepidophylla</i>	<i>Casearia sylvestris</i>
<i>Rhacoma aquifolia</i>	<i>Leucaena glauca</i>
<i>Cissus trifoliata</i>	<i>Hibiscus spiralis</i>
<i>Bourreria revoluta</i>	<i>Metopium brownei</i>
<i>Jacquinia keyensis</i>	<i>Cameraria tomentosa</i>
<i>Stigmaphyllon sagittaeum</i>	<i>Guilandina intermedia</i>
<i>Eustoma exaltatum</i>	<i>Anthacanthus acicularis</i>
<i>Comocladia dentata</i>	<i>Crinum americanum</i>
<i>Pithecellobium prehensile</i>	<i>Calonyction tuba</i>
<i>Neobracea bahamensis</i>	<i>Cakile lanceolata</i>
<i>Amyris elemifera</i>	<i>Pseudocardium ilicifolia</i>
<i>Lantana involucrata</i>	<i>Ipomoea cathartica</i>
<i>Smilax havanensis</i>	<i>Chamaesyce buxifolia</i>
<i>Abrus precatorius</i>	<i>Stachytarpheta jamaicensis</i>
<i>Cordia globosa</i>	<i>Urechites lutea</i>
<i>Banara reticulata</i>	<i>Tribulus cistoides</i>

The Hieacos Peninsula, and Maisi with which this monograph will be closed, are the finest examples of dry coasts in Cuba and among the finest on any Caribbean shore, yet for the sake of completeness and comparison, it might be well to discuss another Cuban strand and thicket, one which Ekman thought the best of the island, the "playa de Maria Aguilar" near Trinidad on the south coast. The writer cannot agree with Ekman that the Trinidad xerophytic association surpasses those of Hieacos and Maisi. Possibly Ekman did not see these latter regions. The plant types on the Trinidad coast are much more intermingled, the associations more confused, the thicket less pure. However, it is in just such regions that one picks up species not common, or missed, elsewhere, as the writer did the widely disseminated and interesting little swamp plant, *Batis maritima* with its small potato-like fruits. Here also was a

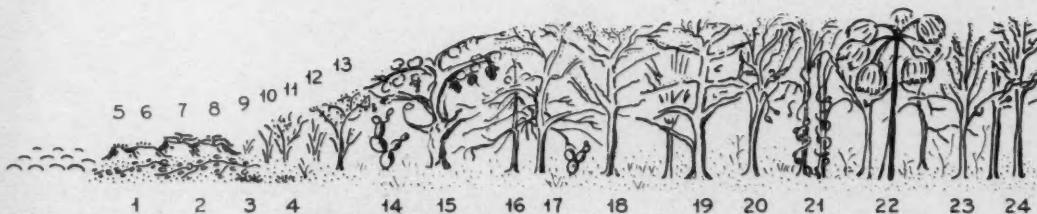


FIG. 13. The plant life of strand and thicket at Varadero (see special legend).

1. *Ipomoea pes-caprae*, 2. *Canavalia maritima*, 3. *Ambrosia hispida*, 4. *Heliotropium curassavicum*, 5. *Philoxerus vermicularis*, 6. *Trianthema portulacastrum*, 7. *Rachicallis americana*, 8. *Conocarpus erecta*, 9. *Uniola paniculata*, 10. *Sporobolus* sp., 11. *Suaeda linearis*, 12. *Suriana maritima*, 13. *Tournefortia gnaphalodes*, 14. *Opuntia dillenii*, 15. *Coccobola uvifera*, 16. *Plumeria alba*, 17. *Pithecellobium prehensile*, 18. *Exostemma caribaeum*, 19. *Caesalpinia vesicaria*, 20. *Guajacum sanctum*, 21. *Stigmaphyllon sagittaeum*, 22. *Coccothrinax littoralis*, 23. *Jacaranda coerulescens*, 24. *Parkinsonia aculeata*.

common Caribbean thicket tree, the legume, *Acacia farnesiana* (Fig. 14), and with it two other legume trees, *Caesalpinia vesicaria*, and *Lysiloma bahamensis*, the latter very widespread on Caribbean shores.

The following list of plants make up the conglomerate association, part strand, part desert, part thicket on the Trinidad coast. They are enumerated as found from the water's edge to a point half a mile inland.

*Rhizophora mangle*  
*Batis maritima*  
*Ipomoea pes-caprae*  
*Canavalia maritima*  
*Suaeda maritima*  
*Tournefortia gnaphalodes*  
*Coccocloba uvifera*  
*Opuntia dillenii*  
*Baccharis halimifolia*  
*Terminalia catappa* (introd.)  
*Coccothrinax miraguana*  
*Leucaena glauca*  
*Cassia lineata*  
*Acacia farnesiana*

*Guilandina crista*  
*Caesalpinia vesicaria*  
*Lysiloma bahamensis*  
*Borreria arborescens*  
*Comocladia dentata*  
*Eragrostis salzmanni*  
*Indigofera tinctoria*  
*Melicocca bijuga*  
*Plumeria obtusa*  
*Tecoma stans*  
*Capparis flexuosa*  
*Solanum bahamense*  
*Bursera gummosa*

At the extreme inner edge of this coastal conglomerate, a mile or more from shore, is a very unusual palm growing on savana-like fields, the short and stodgy *Copernicia torreana* (Fig. 30).

There is much of thicket in Cuba, all of it bears a close resemblance to that on the Hicacos Peninsula,

even to the characteristic palm; but usually there is some variation, and not all thicket is coastal. In Pinar del Rio Province there are inland thickets, less dense and less dramatic than that on the Hicacos Peninsula, but still a typical scrub vegetation of the chaparral type. Such are the arid fields at the northern base of Pan de Guadjaibon, the highest mountain (3,200 feet) west of Habana. Here, the coastal vegetation is a mangrove swamp. Back of it lie fertile cane fields interspersed with royal palms and occasional Ceibas (Fig. 43). Along the ravines grow clumps of the tall wild cane (*Gynerium sagittatum*). Farther back on the slopes of the hills is a forest of *Pinus caribaea*, bordered by a narrow strip of transitional vegetation, a semi-savana or semi-thicket, with the palms *Copernicia* and *Coccothrinax* (Fig. 37). This *Copernicia* is a small but massive palm, as yet unnamed; it is near *C. glabrescens* and *C. pauciflora*. The *Coccothrinax* is the tall and slender *C. miraguana*.

On serpentine outcroppings where pine barrens pass over into more fertile fields, there is a transitional thicket. Dominating these inland thickets are the microphyllous tree-shrubs, *Erythroxylum alaternifolium*, *Anthacanthus tetraspilus*, *Phyllanthus orbicularia*, *Brya ebenus*, and *Buxus leoni*. This arid bush vegetation contains in addition *Byrsinima crassifolia*, the toxic *Comocladia dentata*, *Rondeletia odorata*, *Rhabdadenia paludosa*, *Gymnanthes lucida*, *Smilax havanensis*, *Arthrostylidium capillifolium*, and a *Tillandsia*, probably *T. circinnata* (Fig. 15).

The foregoing thicket merges into pine land forming with it a very heterogeneous association, which will be discussed under savana-woodland.

The thickets so far described are primary. They represent a true evolutionary development, perhaps a climax in plant succession. But there are also pseudo- or secondary thickets, found mostly on waste land. These are not true ecological types, yet they are distinct plant associations.

Much discarded land in Cuba is now over-run by a shrubby growth of the thorny marabú, the mimosaceous *Dichrostachys nutans*, an introduction from Africa. Marabú thickets constitute a form of secondary thicket.

The development of thicket is along one of two evolutionary lines. Either the thicket is a primitive association of plants representing an advance over desert, to be converted into forest in time, or it is a retrograde association of plants on once fertile ground, now degenerate through neglect. The coastal thickets of Cuba are of the first kind and represent a primitive vegetation evolving toward something higher, whereas the marabú thicket is a degenerate community. But when one plant association, developing into something higher, reaches the same stage as another degenerating into something lower, it is difficult to distinguish between the two.



FIG. 14. *Acacia farnesiana* ( $\frac{1}{2}$  life size).

FIG. 15. *Tillandsia circinnata* (½ life size).

## 4. LIMESTONE

## A. COASTAL LIMESTONE

There are many limestone areas in Cuba, chiefly coastal, which are badly eroded coral outcroppings. They are a mass of small, sharp pinnacles and knife-like edges. Walking over them is both tiring and dangerous. The ground is solid calcareous rock with little or no visible soil. Much of this ragged limestone ground is in arid country, such as far eastern Oriente, but even when in relatively moist areas, as in Habana and Pinar del Rio Province, the ground is still very dry owing to the porosity of the coral. The vegetation is, therefore, semi-xerophytic throughout.

Limestone in Cuba is found in two forms, distinct as to place, topography, and vegetation, but alike in constitution of the substratum and in aridity. Outcroppings of limestone occur both as narrow coastal belts, as just described, and as haystack hills or mogotes. The calcareous nature and semi-aridity of the ground are the same in both localities, but topography is sufficiently different to produce quite

unlike plant communities. There are genera typical of each region that are unknown to the other.

The vegetation of the coastal limestone belt is a blend of desert and thicket. It might, therefore, be taken up as a transitional association of plants, but the writer elevates it to a major group, because of its extent and its very characteristic flora. There are a dozen miles of this badly eroded coastal limestone, from Maisi to Mata, and much more elsewhere on the coast and keys of Cuba. Agave is always present and indicates the general character of the association, a mingling of desert and thicket floras on a semi-arid substratum.

The genera which characterize the vegetation of coastal limestone and coral reefs are Clusia, Agave, Hippomane, Plumeria, Comocladia, Cecropia, Eugenia, Metopium, Coccothrinax, Smilax, and the epiphytic orchid *Laeliopsis domingensis*.

Any one superficially familiar with the plant life of Cuba would say, "but these plants are everywhere on the island." That is true. All are widespread; *Clusia rosea*, for example, is found from shore to mountain top.

*Clusia* deserves a moment's additional attention for it is a conspicuous plant throughout the American Indies. Its glossy, leather-like leaves and its strangling habit give it a superficial resemblance to the strangling fig, which causes some confusion in common names. I rather imagine that *Clusia* outdoes all other Caribbean plants in the matter of distribution, except possibly *Cecropia*. Both are found on all the Antilles and the Caribbean mainland. In Guadeloupe and Trinidad, *Clusia* grows from coast to mountain summit. There is a large and dense thicket of it on Mt. Soufrière in Guadeloupe, and on Tucuche in Trinidad. Marie-Victorin and León picture it on the summit of Loma de Goma near Santiago de Cuba.

*Agave*, likewise, is of such wide distribution that it is placed with difficulty except that its habitat, whether at the coast or on sub-alpine rocky crags (Fig. 52) is always an arid one.

The toxic *Hippomane mancinella*, known to Latin Americans as manzanilla and to English colonials as manchineel, is more restricted in its distribution. The writer knows it only near the sea, where it does as well in sand as on calcareous rock. *Plumeria*, also, though typically coastal and on limestone, thrives in fertile garden soil, and there is no more widespread tree along Cuban lowland roadsides than *Comocladia*.

Among these plants the one most restricted to coastal limestone is the anacardiaceous *Comocladia dentata*, called "guao" in Cuba. It is rather common along roadsides but usually only on rocky ground, though occasionally on serpentine rock. *Comocladia* is never on good soil, never on siliceous sandy soil, and though on rocky serpentine it is not on savanas of weathered serpentine soil.

*Comocladia dentata* deserves additional mention because of its toxicity. It is the most dreaded plant in Cuba. Its sap causes inflammation of the skin

much after the manner of *Rhus toxicodendron* in North American. *Comocladia* has one attractive feature, its leaves are quite decorative (Fig. 16).



FIG. 16. *Comocladia dentata* ( $\frac{1}{2}$  life size).

It is now quite obvious that the vegetation of coastal limestone is very cosmopolitan; yet as an association, it is distinctive. The plants are each widespread, yet nowhere else are they all gathered into one society.

#### B. MOGOTE

Mogotes are called haystack hills in Puerto Rico for that is their shape (Fig. 17). They are formed by more rapid weathering of the surrounding terrain



FIG. 17. Vifiales and its mogotes.

which leaves the limestone outcroppings elevated. The precipitous sides of the mogotes make them a very conspicuous, rather dramatic, though somewhat amusing feature of western Cuban landscape (Fig. 18).

In spite of their similar chemical composition, for both are of limestone, the vegetation of the mogotes and the coastal calcareous belt are not identical. On the contrary, they are quite different, thus, the palm *Gaussia princeps*, the malvaceous *Bombax emarginatum* and the rutaceous *Spathelia brittonii*, are always together, forming an inseparable trio on all mogotes, but never on coastal limestone.

These three plants all deserve special mention for reasons other than their occurrence on mogotes. The palm, *Gaussia princeps*, is endemic to the western limestone hills of the Sierra de los Organos. *Bombax emarginatum* is one of the kapok-producing "silk-cotton" trees. Its presence on mogotes is made immediately obvious at a distance by its almost white trunk (Fig. 18). The bulging form of the trunk is likewise a peculiar feature (Fig. 19), and its extraordinary capacity to cling to sheer rock is remarkable (Fig. 20).

Deserving of special mention for quite other reasons is the superb *Spathelia brittonii* (Fig. 1). At a distance it resembles a palm or a tree-fern. It is a beautiful tree, not only because of its form but for



FIG. 18. A limestone hillock or mogote; the white tree trunks are of *Bombax emarginatum*.

its flowers as well; these are small, pink-violet in color, and occur in huge inflorescences.

As on all arid rocky habitats whether lowland or highland, limestone or granite, *Agave* flourishes. On mogotes it is *A. tubulata*.

The following plants are common to mogotes in western Cuba: *Thrinax microcarpa*, *Bombax emarginatum*, *Gaussia princeps*, *Spathelia brittonii*, *Tabebuia lepidophylla*, *Omphalea hypoleuca*, the "roblo caiman" *Ekmanianthe actinophylla*, *Agave tubulata*, *Anthurium venosum*, *Tillandsia capitata*, and species of *Peperomia*, *Piper*, *Pilea*, *Hohenbergia*, *Aechmea*, and *Catopsis*.

The finest of Cuba's mogotes are those at Viñales. "One has not seen Cuba until one has seen Viñales,"



FIG. 19. *Bombax emarginatum* on a limestone hillock at Sumidero; a mogote in background.

is an old saying on the island. Although it is the vegetation of the mogotes themselves in which we are at the moment concerned, the surrounding country at Viñales is of great botanical interest.

From Viñales one may go on to Puerto Esperanza, a simple bustling resort where extensive mangrove swamps line much of the shore (Fig. 9), or preferably to the delightful little village of Sumidero where the real character of the best of Pinar del Rio Province may be appreciated (Fig. 21). The countryside is devoted primarily to tobacco but also in large measure to sugar growing. Nearby are excellent mogotes where all of the above-enumerated plants may be found, in fact, it is at Sumidero that the writer did most of his collecting and where he first saw *Spathelia* (Fig. 1).

Abundant in the neighborhood, but widely spread over Cuba is the rubiaceous tree, *Genipa americana* (Fig. 22). The fruit is much eaten. The common Cuban name of it is jagua.



FIG. 20. *Bombax emarginatum* clinging to the steep slope of a mogote.



FIG. 21. The picturesque and fertile limestone country at Sumidero.



FIG. 22. Jagua, *Genipa americana*.

## 5. SAVANA

### A. IN GENERAL

If the writer were asked to characterize Cuba with one word, that word would be savana. (The Spanish spelling is retained rather than the American "savanna" or the English "savannah," because the word is of Spanish-American origin, probably Venezuelan.) No single formation covers so much territory in Cuba, or is more typical of Cuban landscape than the savana. Cuban savana is usually flat or undulating, non-arable, grass-covered land, often underlaid with serpentine rock. Arability is not a wholly reliable character, for it in large measure depends upon an earnest attempt to cultivate the land; however, Cuban savana is bad land. Bennett and Allison (Fig. 36) in their account of the soils of Cuba refer frequently to arable and potentially arable savana land. Carabia (1940, 1941) refers to dry savanas, moist and better savanas, and rich savanas which are sometimes cultivated. It will be noticed that Carabia, a Cuban, characterizes the rich savanas as "sometimes" cultivated.

For the layman, treelessness is the chief characteristic of the savana, but for some ecologists it is pre-

cisely a few scattered trees which differentiate savana from prairie and steppe. Lack of fertility distinguishes savana from meadow.

The word savana was first put into print in 1535 by Oviedo in his classical "La Historia Natural y General de las Indias" (Seville, 1535). When the word was introduced into Spain it came to mean any extensive grassland. Dictionaries generally define savana as a treeless plain, thus making it equivalent to prairie and steppe; but Zayas in his "Lexicographia Antillana" says "sabana" is a "word of the Indians of Haiti and Cuba, characterizing an extensive flat land, not fertile, and with very few trees." This is also Schimper's interpretation. Humboldt described the llanos of Venezuela as treeless plains or savanas, and to this Schimper objected. He found the llanos not treeless but park-like, a grass-covered plain seantly dotted with solitary trees. Schimper thus distinguishes savana, which is xerophilous grassland with isolated trees, from steppe which is treeless, and from meadow which is hygrophilous grassland. To this the writer agrees, and rare is the Cuban savana without its palms, some of which are tall and noble trees (Figs. 23, 60). Llanos, campos, and paramos are other savana-like areas the precise meaning of which will depend in part on local usage.

As for the fertility of savanas, the matter is left to the Cuban for it is his country. In the main savanas are not of good soil; they are often of serpentine and rarely make good pasture, for the grass is coarse and wiry. This fact is illustrated in an old Cuban saying: On bad land there is good water and on good land the water is bad. It is on savana that the best spring and well water is to be had.



FIG. 23. *Sabal floridana*.



FIG. 24. Sabal savana in western Cuba.

Savana palms are primarily *Sabal* (Fig. 24), often *Copernicia* (Fig. 30) and *Coccothrinax* (Fig. 32), but never *Roystonea*. The royal palm grows on fertile ground, on limestone soil in meadows, with the *Ceiba* (Fig. 43) and *saman*, or in arable fields with sugar cane (Fig. 42) and tobacco, but not on savana land.

Royal palms scattered over meadow land present typical savana country to a visitor, for there is grass with scattered trees, but here the course of events has been altered by man. The land is no longer a natural area; it has been cleared to make pasture. A rich meadow is not usually a natural area. Were it so it would be forest and not savana.

In Cuba there are numerous kinds of savana, such as palm savana, bushy savana, and sandy savana. A "sao" is a small savana surrounded by woods. All have the poverty-stricken appearance of poor land (Figs. 24, 34).

The term savana is therefore best used for grass-covered, non-agricultural land with scattered trees, thus differentiating it from all arable fields, meadows, and pastures.

As the savanas of Cuba may be distinguished by soil and vegetation, it would be convenient to discuss them as either soil or vegetational types. These, they are, but though sharp contrasts in both vegetation and soil exist, there are enough similarities between savanas, and between savanas and other regions, to confuse the situation. Thus, there is no more characteristic plant of the Pinar del Rio savana than the *Sabal*, and this palm is almost wholly lacking from the savanas of eastern Cuba. What, therefore, appears to be a distinction between the Occidental and the Oriental savana palms of Cuba is nullified by the very wide distribution of the *Sabal* in all parts of the island quite apart from savanas. The writer attempted a similar distinction on the basis of the grasses of western Cuba. There seemed to be a great abundance of *Panicum*, *Paspalum*, *Aristida*, and *Andropogon* on the western savanas of Cuba, but these genera are in all provinces.

In spite of difficulties in making sharp distinctions it is yet true that some Cuban savana plants have an east-west distribution, several being endemic. The

palm illustrate this if taken as a group. Though there is much overlapping, they distinguish the occidental savanas from the oriental, with *Sabal* (Fig. 23) very typical of, and *Colpothrinax* (Fig. 25) wholly restricted to the Pinar del Rio savanas. Certain species of *Coccothrinax* are limited in distribution though the genus is widely distributed. In western Cuba is *Coccothrinax yuraguana*. In central Cuba, on the coast, is *C. littoralis*. On the savanas of Camagüey and Holguin grows *C. muriata*. *C. victorini*, *C. saxicola*, *C. grundlachii*, *C. fragrans*, and *C. alexandri* (Fig. 60), are all on savana ground in far eastern Cuba.

Equally difficult is the differentiation of the savanas of Cuba on the basis of their soils. Some pronounced differences exist, thus the western savanas are primarily siliceous whereas the eastern savanas are mostly serpentine. A careful study, however, reveals that too sharp a distinction cannot be made. The analysis of savana soils by Bennett and Allison (Fig. 36) shows how exceedingly confusing an interpretation of vegetational differences in terms of soil composition can be. It seemed, therefore, in the case of Cuba better to select a purely arbitrary grouping of the savanas, namely a geographic one based on provinces. This may appear to be artificial, but actually it adheres closely to the natural characters of Cuba's savanas. No careful study is necessary to distinguish Pinar del Rio country from that of Habana, Camagüey, and Oriente. Scenically and agriculturally they are unique. Pinar del Rio is adapted to tobacco growing, Habana is garden country, Camagüey is the cattle-grazing province of Cuba, and Oriente is a land of forests.

A review of Cuba's savanas by provinces will make the writer's task easier, and our journey less confused, but we shall not, therefore, hesitate to make an analysis of the possible edaphic causes underlying differences in vegetational types.

#### B. PINAR DEL RIO

As the general trend of our journey is from west to east, we may start with the Pinar del Rio savanas. They are principally siliceous sandy soils, with some clay, and all of poor or mediocre agricultural value. Their dominant plant is the *Sabal* palm (Fig. 23), usually *Sabal florid*.

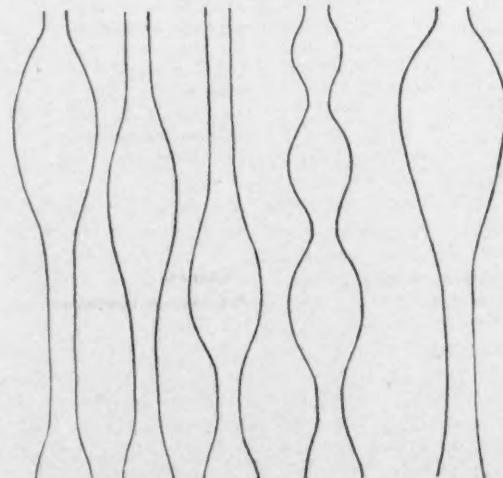
A well-developed *sabal* savana is an impressive sight. It becomes a somewhat amusing one when the *sabals* have been plucked for thatching; they then resemble a lot of game cocks after a fight (Fig. 24).

The *Sabal* dominates the western savanas; in this sense it characterizes them. But the *Sabal* is so widespread that one must turn to some other plant by means of which to distinguish the savanas more specifically. This is not too difficult because several endemics grow on occidental savana land in Cuba. Notable among these is the belly palm, which the English, who allow less of the picturesque in their language than do the Spanish, call the bottle palm; it is *Colpothrinax wrightii* (Fig. 25). This palm

FIG. 25. *Colpothrinax wrightii*.

was formerly *Pritchardia*, so named by Beccari, thus establishing a relationship with the Polynesian belly palm, but Hermano León is convinced that it is not a relative of the Old-World *Pritchardia*, and should therefore come under the genus, *Colpothrinax*.

The swelling of *Colpothrinax wrightii* presents an interesting and as yet unsolved problem as to why palms swell. An occasional palm, yes, a pathological situation would account for it; but when all specimens of a species swell, an interpretation is difficult, except on the basis of a generic factor. That the swelling of *Colpothrinax* is genetically determined is suggested by the uniformity of its size and position. On the other hand, the frequency of irregular swellings midway on the trunks of royal palms when in the wild state, and their absence on royals grown under cultivation suggests that the bulge may be an ecological character determined by soil qualities. All royals flare at the base and bulge slightly at the top but most specimens are straight midway between top and bottom (Fig. 26), which means that the basal and apical swellings are generic characteristics whereas the central ones are not. The trunk of *Aeroecomia* is usually carrot shaped; this is very

FIG. 26. Swellings on trunks of royal palms and, extreme right, an *Aeroecomia*.

likely a species characteristic. We may then conclude that the basal and apical flare of the royal, the conical shape of *Aeroecomia*, and the bulge of the belly palm are so uniform in position, and so persistent that they give every evidence of being a generic quality, whereas the centrally located, irregular and sporadic swellings of the royal palm in the wild state are probably due to purely physiological factors. Possibly the whole question is one of those instances where inheritance and environment are so interdependent that there is no distinguishing them; both are necessary for the development of a characteristic.

The following plants are typical of the siliceous savanas of Pinar del Rio:

## PALMS

*Sabal floridana*  
*Colpothrinax wrightii*  
*Copernicia glabrescens*  
*Acoelorrhaphes wrightii*

## SHRUBS

*Byrsinima crassifolia*  
*Rondeletia correifolia*  
*Miconia delicatula*  
*Tabebuia lepidophylla*  
*Curatella americana*  
*Vaccinium ramontii*  
*Befaria cubensis*  
*Kalmiella ericoides*

## GRASSES

*Paspalum pulchellum*  
*P. plicatulum*  
*Aristida refracta*  
*A. neglecta*  
*Cenchrus distichophyllus*  
*Sporobolus purpurascens*  
*Andropogon virginicus*  
*Panicum condensum*  
*Trachypogon filiformis*  
*Imperata brasiliensis*

## SEDGES

*Dichromena ciliata*  
*Rhynchospora globosa*

Where the savana land is moist there are numerous species of Cyperaceae, Xyridaceae, Eriocaulaceae, Droseraceae, Polygalaceae, and some Compositae.

## C. THE ISLE OF PINES

The Isle of Pines is geologically and ecologically part of Pinar del Rio Province. The similarity is evident in the savana floras, and in the mogotes or limestone hillocks so characteristic of Pinar del Rio.

That the Isle of Pines is floristically a part of Pinar del Rio is shown by the presence in both, and not elsewhere in Cuba, of several endemics such as the occidental Cuban pine, *P. tropicalis*, and the palm, *Colpothrinax wrightii* (Fig. 25). Numerous plants which are dominant or abundant in Pinar del Rio are also common to the savanas of the Isle of Pines; these include the palm, *Acoelorrhaphes wrightii* (here given the varietal name, *novogeronensis*), and the microphyllous shrubs *Erythroxylon* and *Brya*.

The palms of the Isle of Pines number some six species of which one, *Copernicia curtissii* is endemic. It resembles a *Sabal* except for extraordinarily long rachises.

*Acoelorrhaphes wrightii* presents an interesting biological problem. It has the habit of forming "witches' rings" (Fig. 27). Depletion of nutrition within the rings has been given as an explanation, but this is inadequate. More likely the ring is due to the rhythmic growth of a rhizomatous system.

The savanas of the Isle of Pines though barren in general appearance are rich in vegetation. They



FIG. 27. Acoelorraphe "witches' rings."

differ from the Pinar del Rio savanas in their closer resemblance to heath. Myrsina and Kalmiella are common Ericaceae on the Isle of Pines. *Kalmiella ericoides*, with its familiar laurel flowers, is an endemic, so also *Aristida brittonorum*. *Helenium scaposum* is another endemic corresponding to *H. tenuifolium* in similar areas in Pinar del Rio. Typical of the Isle's savana flora are *Croton trigonocarpus* and the delightful *Hypericum stypheleoides* (Fig. 28). Conspicuous and abundant are Hibiscus, Cassia, and Pithecellobium. The predominating grasses are *Andropogon virginicus* and an *Aristida*.

But it is another plant to which special attention should be called, the diminutive eyead, *Zamia silicea*

FIG. 28. *Hypericum stypheleoides*.FIG. 29. *Zamia silicea* on the Isle of Pines.

(Fig. 29). It is a feature of the vegetation of the siliceous savanas of the Isle of Pines. Unlike other members of the family it is a true open savana plant, but its greatest appeal lies in its size, for it is one of the smallest of eyeads, rising scarcely more than six inches off the ground, with three or four horizontal twelve-inch leaves and a small tap root.

As the vegetation of the Isle of Pines grades imperceptibly from savana into heath, thicket, and open woodland, it is futile to attempt to group the plants ecologically. The following is a representative flora of the Isle of Pines:

PALMS	SHRUBS
<i>Colpothrinax wrightii</i>	<i>Rondeletia correifolia</i>
<i>Copernicia curtissii</i>	<i>Brya ebenus</i>
<i>Acoelorraphe wrightii</i>	<i>Byrsonima crassifolia</i>
<i>Coccothrinax miraguama</i>	<i>Hibiscus costatus</i>
var. <i>arenicola</i>	<i>Kalmiella aggregata</i>
<i>Sabal floridana</i>	<i>Eriocaulon scirpoides</i>
<i>Calyptrochoma dulcis</i>	<i>Hypericum stypheleoides</i>
	<i>Malpighia</i> sp.
	<i>Suriana maritima</i>
TREES	<i>Cassia hispida</i>
<i>Pinus tropicalis</i>	<i>Pithecellobium hystrix</i>
<i>Genipa americana</i>	<i>Myrica cerifera</i>
<i>Curatella americana</i>	<i>Smilax havanensis</i>
<i>Paritium tiliaceum</i>	<i>Jussiaea peruviana</i>
<i>Cecropia peltata</i>	<i>Jatropha angustifolia</i>
<i>Chrysobalanus pellocarpus</i>	
<i>Tabebuia lepidophylla</i>	
<i>Rhizophora mangle</i>	
<i>Avicennia nitida</i>	
HERBS	FERNS
<i>Pinguicula filifolia</i>	<i>Alsophila aspera</i>
<i>Hyptis brevipes</i>	<i>Dryopteris sclerophylla</i>
<i>Nymphaea advena</i>	<i>Blechnum serrulatum</i>
<i>Polygala cubensis</i>	
<i>Drosera rotundifolia</i>	
<i>Phoradendron antillarum</i>	
<i>Melochia nodiflora</i>	
<i>Opuntia dillenii</i>	
<i>Xiphidium xanthorrhizum</i>	
ORCHID	SEDGES
<i>Tetramicra euphiae</i>	<i>Rhynchospora globosa</i>
	<i>Stenophyllum paradoxus</i>
GRASSES	
<i>Andropogon virginicus</i>	
<i>Aristida neglecta</i>	
<i>Olyra latifolia</i>	
<i>Eragrostis cubensis</i>	
<i>Reynaudia filiformis</i>	

## D. HABANA AND MATANZAS

Much of Habana, Matanzas, and western Santa Clara Province is devoted to agriculture, and to so great an extent that on the writer's first visit to Cuba he made but few notes of the natural vegeta-

tion of these provinces. Matanzas clay is excellent arable land, and Habana clay good. As a large portion of these provinces is in a state of cultivation the savanas are less distinctive than those to the west and east, but they may yet be characterized, and principally by their palms. The following are common on Habana and Matanzas savanas:

- Copernicia torreana*
- C. hospita*
- C. glabrescens* var. *havanensis*
- C. ramosissima*
- Sabal florida*
- S. parviflora*
- Acoelorrhaphis wrightii*
- Coccothrinax miraguama* var. *havanensis*
- C. miraguama* var. *rosea*

The first of these, *Copernicia torreana*, is abundant on coastal serpentine savanas. It is a very striking plant (Fig. 30) and a fine example of the great variety in palms which Cuba harbors.

*Acoelorrhaphis* reaches its eastern limit in Matanzas Province; it is sharply confined to territory west of the River Zaza.

*Yucca aloifolia*, often in magnificent flower, *Fera-cacia daemon*, *Croton trigonocarpus*, and *Andropogon*

*virginicus* are frequent inhabitants of the central Cuban savanas.

#### E. CAMAGÜEY

The Camagüey savana is not luxuriant in vegetation, in fact it is a rather dreary plain, but its dominant species are unique. The vegetation of the savana is full of surprises for the newcomer; the palms alone justify a visit, not for their beauty but because they are unlike anything else in the Antilles. They are:

- Copernicia hospita*
- C. cowellii*
- C. baileyana*
- Coccothrinax miraguama*
- C. pseudorigida*
- C. pseudorigida* var. *acaulis*

*Copernicia cowellii* (Fig. 31), like *C. torreana*, retains its dead leaves for years, compressed against the trunk much after the manner of *Washingtonia* in southern California.

*Coccothrinax pseudorigida* and its varietal form were, by some botanists wrongly referred to *C. rigida*, but this species grows in the Sierra de Nipe and not on the lowland savanas of Oriente. The species on the Camagüey savana presents an extraordinary ecological problem in that there are two forms identical



FIG. 30. *Copernicia torreana*.



FIG. 31. *Copernicia cowellii*.

in all respects except size. The one is moderately tall but seldom exceeds 12 feet; the other is dwarf, rarely over 18 inches high. The fan leaves of the two do not differ greatly in size. These two varieties, wrongly referred to as *C. rigida*, have recently been separated by Hermano León into *C. pseudorigida*, which is the tall variety (Fig. 32), and *C. pseudorigida* var. *acaulis*, the stemless one. That the dwarf form is mature is evident from the fruit it bears (Fig. 33).

We speak of ecological or growth forms and assume that each is an ecological type, evolved by and adapted to its environment. There are many examples to support this view, but there are as many to disprove it; and one of them is the coexistence in the same environment on identical soil of two forms of a palm formerly regarded as one and the same.



FIG. 32. *Coccothrinax pseudorigida* on the Camagüey savana.



FIG. 33. The dwarf *Coccothrinax pseudorigida* var. *acaulis*; note fruit.

It seems quite impossible that the two varieties of this palm, now known as *C. pseudorigida* and *C. pseudorigida* var. *acaulis*, growing side by side as shown in Fig. 32, are due to edaphic factors.

Another remarkable palm among the half dozen species which thrive on the Camagüey savana is *Copernicia baileyanana*. It is a tall palm, 40 feet, with a closely oppressed crown of fan leaves.

The savana floor is covered by numerous stiff, woody shrubs including *Cassia occidentalis*, *Mimosa pudica*, *Malpighia* sp., the thorny leaved *Anastraphia cowellii*, a Croton, a Plumeria, and the unusual, small *Coccoloba cowellii*.

#### F. ORIENTE

To the east of the Province of Camagüey lies Oriente. An arm of the Camagüey savana reaches over into Oriente where it touches a narrow strip of Miocene limestone and marl. Beyond is an igneous outcropping surrounding the city of Holguin. This is the Holguin savana.

The highest knoll on the undulating surface of the Holguin savana is the Cerro del Fraile. The view from it to the east and west (Fig. 34) reveals a vast semi-barren plain.

Not unlike the Camagüey savana in general appearance, that of Holguin is yet sharply distinguished from it by a number of plants, notably a small scrubby palm, a *Coccothrinax*, recently given the name *C. garciana* by Hermano León (Fig. 34). With it occurs the small, *Copernicia yarey* (Fig. 35). *Sabal floridana* reappears in sparse quantity on the siliceous Holguin savana—it was absent on the serpentine Camagüey savana.

Although the usual savana grasses of Cuba, *Andropogon virgatus*, *A. gracilis*, *Leptocoryphium lanatum*, *Sporobolus indicus*, and *Panicum*, of which there are eight species, are to be found on the Holguin savana, yet the ground cover is by no means the expected grassy carpet, instead it is a rather dense growth of small shrubs, in part thorny, forming a kind of open and low chaparral. In this association are *Pictetia*



FIG. 34. The Holguin savana with the scrub palms *Copernicia yarey* and *Coccothrinax garciana*.

*marginata*, *Ouratea agrophylla*, *Phyllanthus orbicularis*, *Eugenia*, *Jacquinia*, *Heliotropium humifusum*, *Cephalocereus*, and an unidentified *Agave*.

A most unusual plant of the Holguin serpentine savana is the miniature cactus, *Coryphanthus cubensis*. It forms a small knob close to the ground. The average total length is but 2 inches and of this less than half is above soil.

Floristically the savanas of Camagüey and Holguin differ strikingly from those of Pinar del Rio. This is shown best in the palms of the two regions. *Acoelorrhaphis wrightii* and *Colpothrinax wrightii*



FIG. 35. *Copernicia yarey* on the Holguin savana.

are not found in oriental Cuba, and several *Copernicias* common in Camagüey are not to be found in occidental Cuba. The writer has said that the edaphic and climatic factors responsible for the difference in the savana floras of occidental and oriental Cuba cannot be named with certainty, though soil is probably the determining factor. Age does not likely play a part as both Pinar del Rio and western Camagüey are post-upper Miocene. Soil aridity is in part responsible for savana land, but it does not distinguish between savanas. Aridity is often a matter of soil texture.

Serpentine soil is compact, water runs off readily. The savana soil of Pinar del Rio is loose, water runs through it easily. Both soils are, therefore, relatively dry. That texture and resulting aridity is a factor in making savana soil is indicated by land in Camagüey. The surface lies over Guines limestone which elsewhere in Cuba produces excellent ground, but in Camagüey, due to high porosity and lack of accumulated soil, it permits water to run through freely, and aridity results. Thus may soil texture and resulting aridity determine savana vegetation.

Soil composition is the most likely factor responsible for the vegetation of savanas, yet in what way it functions it is difficult to say. Bennett and Allison have prepared an excellent soil map of Cuba which is here reproduced in a slightly simplified form (Fig. 36). Some general facts of help in explaining vegetational types can be extracted from the map of Bennett and Allison, and from work by R. H. Palmer.

The soil of the savanas of Pinar del Rio is a loose quartz sand derived and transported from the Cayteano formation in the Organos Mountains. It contains little plant substance. The soil of the savanas of eastern Camagüey, on the other hand, is formed from residual matter derived from serpentine. There is a high percentage of magnesium—serpentine is a hydrous magnesium silicate. But soil equally rich in magnesium outside of the serpentine area in Camagüey is fair to good agricultural land. Lack of phosphorus, which is characteristic of serpentine, is likewise not responsible for the savana flora. Areas with less phosphorus, as well as those with five or six times as much, produce good vegetation.

Though the distinction in soil composition which is responsible for differences in savana vegetation is not always clear, yet for Cuba this much may be said with certainty: the eastern half of Camagüey has many square miles of serpentine and related rocks and tuffs. Holguin is on a large igneous outcrop, whereas in Pinar del Rio igneous rocks make patches only.

#### G. SAVANA-THICKET

There is much waste land in Cuba which is not true savana. It is a transition from savana to thicket or woodland, either an evolutionary transition, a plant succession, or a grading over due to the intermingling of savana plants with plants from adjoining communities. Such transitional savanas are of



## THE SOILS OF CUBA

(FIG. 36.) This map is a modification of that by Bennett and Allison (The Soils of Cuba, H. H. Bennett and R. V. Allison, Tropical Plant Research Foundation, Washington, D. C., 1928).

## Clays

A == Havana clay; fair soil suited for pasture and henequén.  
 B == Matanzas clay; excellent soil adapted to many crops, extensively used for sugar cane.  
 C == Sandy loam used mostly for tobacco and vegetables.  
 D == Sandy soil and clay; hilly, poor, thin, grassed lands.  
 E == Coastal water-plain soils of considerable variety; in part good clay loam, but much salty flats and hogwash clay lands of poor quality.  
 F == A variety of clay soils, some of good quality.  
 G == Heavy clay soil of poor quality.  
 H == Nipe clay; very poor soil but rich in iron.

## Savanas

K == Serpentine savana.  
 L == Sandy savana; certain of these sandy savanas, as on the Table of Pines, are suitable for citrus fruits and vegetables, if fertilised.

## Limestone

M == Gravelly savana.  
 N == Clay savana.  
 P == Limestone covered with sandy loam; fair soil.  
 Q == Limestone rock; badly eroded with no surface soil but abundant holes with soil below; known as Piedra hueco (hollow stone), and in English as dogtooth limestone.  
 R == Roush, in part mountainous, land of mogote limestone character, some igneous rocks; much forested, suitable for timber, coffee, fruit, and cane.

## Mucilaceous

S == Mountain land, mostly igneous, forested, with small areas of arable land.  
 T == Pine lands, sandy soil of poor quality.  
 U == Stony ground; mosaic of limestone, igneous, and dune sands; suitable for henequen only.  
 V == Peat  
 W == Swamp.

numerous kinds. It is difficult always to distinguish and to name these transitional associations, for often savana, desert, thicket, and woodland are thoroughly intermingled but at times the transition has a real identity. Such is the savana-thicket. In its simplest form it is best represented by savanas near Sancti Spiritus where the legume *Belairia mucronata*, a microphyllous xerophyte, is abundant. With it occurs the subdominant *Byrsinima crassifolia*.

#### H. SAVANA-WOODLAND

In Pinar del Rio Province and on the Isle of Pines are extensive areas of grassland with widely scattered pine trees. The association is a transition, an early stage of forest development. What was grass savana with occasional invading pines has become a thin woods, a savana-woodland. Viewed in the light of plant succession, time may be the factor. In the present instance, however, soil is responsible, thus giving support to the oft repeated dictum of the Swiss botanist, Robert Chodat: in studying plant distribution look beneath the ground. The pine and wire-grass on the Guane sandy loam of the Piedmont Section of western Cuba prove the soundness of this advice, for here the soil is strongly acid. Where the soil is less acid oak replaces pine.

The pine lands are unfit for grazing or agriculture, henequen growing offers the best possibility.

The pines of occidental Cuba are the familiar *Pinus caribaea* which is common in Florida and *P. tropicalis* which is endemic to western Cuba. Both of these species are restricted to the lowland sandy savanas of Pinar del Rio and the gravelly savanas of the Isle of Pines. The pine of oriental Cuba is the endemic *P. cubensis*. It is often the sole arborescent plant on upland territory in Oriente, as on the highlands of Nipe where the soil is of red clay. The serpentine savanas of Camagüey are devoid of pine.

Pines are generally so widely distributed that a determining factor seems to be out of the question. But two there certainly are, competition and soil. Competition is the chief factor in the distribution of pine, and soil a secondary one. The writer has found this true in regions as far removed as the American tropics, the Caucasus, and eastern Turkestan. Pine is generally on bad land, but not by "preference." The pine is anti-social. It cannot stand competition, and so, in seeking isolation, it is forced to survive on poor soil. This it does successfully, for it is a tough and resistant tree. Pine seedlings resist cold well which permits the tree to go farther north, and higher on mountains, than most trees. Its tolerance of dryness and its preference for light serve it well on dry mountain ridges and poor lowland soil where it can thrive without competition. And that is where pine is found. There are square miles of dry undulating land in Pinar del Rio on which pine is the only arborescent plant. They are a reminder of the Carolinian and Georgian coastal plains, for in both countries the pine lands are of poor and acid soil.

Ordinarily, it is first competition, then soil which determines the distribution of the pine, but moisture may also be a deciding factor. This gave rise to an amusing controversy among Russian foresters. The northern slopes of the Main Caucasus Range are wet and support beech and maple to the exclusion of pine which grows on the opposite, southern slopes, in soil too dry for deciduous trees. In the South or Minor Caucasus the southern slopes are too dry for any arboreal vegetation, even pine, but northern slopes are moist enough for pine though too dry for beech and maple; consequently, pine grows on the northern slopes of the Minor Caucasus. When the Russian foresters foregathered to discuss reforestation, those from Russia in Europe wanted to plant pine on southern slopes, but the Georgians insisted on the northern slopes. Both were right for their respective countries.

Pine lands are the most extensive examples of savana-woodland in Cuba but in western Cuba there are thin oak woods on savana land as well. The tree is the southern live oak, *Quercus virginiana*. Like the pine, it is often the sole arborescent plant on hilly savanas of Pinar del Rio. The oak-savanna-woodland is also a transitional association, savana which is becoming forest. In a more advanced stage other plants join the association, particularly ericaceous shrubs such as *Vaccinium ramonii*, *Befaria cubensis*, and *Myrica cerifera*. Such a community is usually on low gravelly soil or "sable."

Whether oak or pine shall predominate in the mixed association on savana is determined by soil acidity; on more acid soil pine stands alone, on less acid soil, oak enters and may wholly replace the pine.

As the savana-woodland becomes more and more heterogeneous, the last trace of savana is finally lost. One may take such a conglomerate as the highest development of the savana in its transition to forest.

#### I. SAVANA-CONGLOMERATE

The savana-woodland transitional areas of western Cuba may become a very heterogenous plant group comprising pine, palms, and microphyllous shrubs (Fig. 37). Such associations are found on the foot-hills of the Organos Mountains. The xerophytic conglomerate character of this vegetation is shown by the presence of savana plants such as *Sabal*, meadow types like *Roystonea*, heath plants such as *Vaccinium* and *Myrica*, limestone inhabitants such as *Agave* or *Furcraea*, the thicket shrubs *Buxus* and *Brya*, and epiphytic bromeliads such as *Tillandsia pruinosa* (Fig. 38), the character of which clearly indicates a xerophytic habitat.

A similar savana-woodland conglomerate occurs on arid western Cuban sandy savanas (Fig. 39). The illustration in Fig. 39 is near Consolacion del Sur in Pinar del Rio. The plant community here is characterized by *Microcybeas calocoma*, *Metopium tomentosum*, *Eugenia buxifolia*, *Plumeria*, *Furcraea cubensis*, *Vanilla eggersii*, *Smilax domingensis*, and *Tillandsia paniculata*, all visible in Fig. 39.



FIG. 37. The pine-palm savana-woodland of western Cuba.

The arid western Cuban savana-thicket-woodland transition contains:

<i>Sabal florid</i>	<i>Erythrina cubensis</i>
<i>Roystonea regia</i>	<i>Eugenia buxifolia</i>
<i>Copernicia glabrescens</i>	<i>Metopium toxiferum</i>
<i>C. pauciflora</i>	<i>Plumeria sericeifolia</i>
<i>Acocelorrhapha wrightii</i>	<i>Vaccinium ramonii</i>
<i>Colpothrinax wrightii</i>	<i>Furcraea cubensis</i>
<i>Calyptrotroma dulcis</i>	<i>Ambrosia peruviana</i>
<i>Thrinax microcarpa</i>	<i>Anthurium crassinervium</i>
<i>Coccothrinax miraguana</i> var. <i>arenicola</i>	<i>Philodendron wrightii</i>
<i>Pinus caribaea</i>	<i>Billbergia penduliflora</i>
<i>P. tropicalis</i>	<i>Tillandsia pruinosa</i>
<i>Quercus virginiana</i>	<i>T. paniculata</i>
<i>Phyllanthus orbicularis</i>	<i>Bromelia pinguin</i>
<i>Brya ebenus</i>	<i>Byrsinima crassifolia</i>
<i>Buxus leonii</i>	<i>Maxillaria</i> sp.
<i>Rhabdadenia cubensis</i>	<i>Arthrostylidium capillifolium</i>
<i>Bondeletia odorata</i>	<i>Gynerium sagittatum</i>
<i>Gymnanthes lucida</i>	<i>Microcycas calocoma</i>
<i>Smilax havanensis</i>	<i>Conocladia dentata</i>
<i>S. dominicensis</i>	<i>Erythroxylon alaternifolium</i>
<i>Vanilla eggersei</i>	<i>Anthacanthus tetrastichus</i>
	<i>Notolena</i> sp.



FIG. 38. *Tillandsia pruinosa* (1/2 life size).

For botanists, the outstanding plant of this association is the eyead *Microcycas calocoma* (Fig. 40) of which three specimens are visible in Fig. 39.

The cycads of the western hemisphere are *Zamia*, *Microcycas*, *Dioon*, and *Ceratozamia*. Two of these, *Microcycas* and *Zamia*, are natives of Cuba. In spite of its name, it is not the former but the latter which is a small eyead; indeed, *Microcycas* is exceeded in size by only two other cycads.

*Microcycas* is endemic to Cuba. There is, as yet, but one species, in Pinar del Rio, *M. calocoma*. Certain of the isolated plants may, however, prove to be other species. The best specimens of *Microcycas* are in the mountains of Pinar del Rio, though there is one venerable specimen near the group pictured in Fig. 40. It has fallen, but lives on in a prostrate position. It is forked, and some 40 feet long, surely a century old.

Of *Zamias*, several species are native to Cuba: the diminutive *Z. silicia* on the Isle of Pines; *Z. latifolia* which, though not abundant, is widespread occurring both in eastern Oriente and western Pinar del Rio; *Z. kickxii*, a doubtful species restricted to Habana Province; *Z. media* or *Z. angustifolia* also doubtful and credited to the Hicacos Peninsula; and *Z. pygmaea* of the savanas of Pinar del Rio.

*Microcycas* is the rarest and geographically most restricted plant of all Cuba. It is an endemic attributed to late Jurassic or early Cretaceous and occurs only between San Diego de los Baños on the east and Sumidero in Pinar del Rio Province on the west.

FIG. 39. Several specimens of *Microcycas calocoma*

It would be a hopeless task to single out each savana land and discuss it as a type. Many small igneous outcroppings in Cuba are diminutive savanas. But there is one plant association in Cuba which is quite savana-like in character, assuming the importance of a major soil and vegetational type. The soil is truffin clay, second only to Matanzas clay in extent. On it grows *Acrocomia crispa* (Fig. 41), called corojo in Cuba, palma cana, which is *Sabal florida*, and the star apple (*Spondias mombin*). None of these occurs on true serpentine savana. They form a community on truffin clay.

*Aeroecomia* is one of the most widely spread of Caribbean palms. It will grow most anywhere, but it is usually on open savana land. Though called corojo in Cuba, its better known West Indian name is gru-gru. Its swollen trunk resembles an inverted bottle. Trunk shape, a thorny armor, and the disheveled appearance of its crown are very typical of the palm (Fig. 41).

The most familiar specific name of *Aeroecomia* is *aculeata* which was thought to be common throughout the Antilles including Cuba; but now, according to Bailey (1941), *A. aculeata* is endemic to Martinique and Dominica. Nearly all of the remainder of the West Indies have their endemic species. In Cuba it is *Acrocomia crispa*, though Hermano León has recently reported *A. pilosa* on the hills above Maisi.

#### 6. THE CULTIVATED LANDS

The geological map of Cuba shows large areas of Miocene and Eocene limestone and marl alternating rather regularly with the igneous serpentine and siliceous substratum of savanas. These non-igneous areas are at times narrow, as in western Oriente and eastern Camagüey, and at times very extensive, as in western Camagüey, Matanzas and Habana Provinces. They are the agricultural lands of Cuba. Upon them are grown most of the island's crops, among which meadow-grass, grain, bananas, pineapples, tobacco, and cane predominate.

A discussion of the ecology of vegetation on fertile limestone soil in a populated country is, in great measure, an account of the agriculture of the land, but this is as much a problem in ecology as is a description of the natural flora. Plant geographers and ecologists are inclined to ignore all recent activities of man which have helped determine the plant

FIG. 40. *Microcycas calocoma*.

FIG. 41. *Acrocomia crispa*.

life of a country, but they unwittingly take into consideration similar activities which took place centuries ago. There is very little of the earth's surface the plant life of which has not been influenced by man. The tremendous part played by grazing, deforestation, and land reclamation are but a few examples of man's role in determining the present vegetation of the earth. After all, man is as much a part of the natural scheme of things as is the worm in the soil and the insect upon which the pollination of a plant depends.

The influence of man in the ecology of plant life is best seen in his destruction of some species and his introduction and protection of others. Many of the most familiar domestic trees on Caribbean shores are introduced, the mango, the legumes *Albizia* and *marabú*, and the decorative fig trees. Were a native of Cuba told that these trees were not of his land, he would doubt the veracity of the speaker.

Virgin land may present a more interesting study in ecology than a field planted with *Zea mays*, yet if that field is allowed to "go wild," the plant life on it

a century later is as significant a problem as was the study of the original flora, for the vegetation will be quite other than it would have been had the field been handled differently, quite other if grazed rather than cultivated, quite other if goats rather than cows were grazed.

Little, if any, of Cuba's flat arable land of good quality has been left uncultivated, and much of Cuba's soil is highly productive. Matanzas clay (M. Fig. 36) is particularly rich agriculturally. The Agabama Valley leading from the central plain to the city of Trinidad and passing through the Trinidad Mountains (Fig. 54), impressed the writer as one of the most delightful and prolific farming countries to be seen anywhere in the American tropics. The largest continuous agricultural area in Cuba is the Matanzas Plain of red soil. It extends from the town of Artemisa to eastern Matanzas, thus including most of Havana and Matanzas Provinces. The Plain is on the whole flat and low, large portions of it not rising over 50 feet above the sea. The soils are ferruginous and predominantly red in color. They have been called clay, clay-loam, and loam; Bennett and Allison regard them as a pure and finely grained clay. The soil is excellent agricultural land, some fields having been in cultivation for a hundred years without fertilization.

Of cultivated land in Cuba, almost half is devoted to sugar. Tobacco and bananas come next in quantity produced, then pineapples and maize. These are the great export products of Cuba, with sugar far surpassing all others. Cuba's sugar output has frequently reached a million tons a year and at one time equalled a quarter of the world's total cane sugar production, or a tenth of the total output of the world. Among plants grown for home use, the starchy vegetables include malanga (*Colocasia*), sweet potatoes, yams, beans, cassava, plantain, and tomatoes. Rice, as on most Antillean islands, is a starchy food imported in great quantity. Other crops of only local importance are coffee and a great variety of fruits, bananas being the only fruit exported in any appreciable quantity.

The native fruits of Cuba constitute an interesting chapter. The list is a long one, as can be judged from a glance at the fruit stands in Havana, or at a list of the flavors offered for "refrescos" made from fruit juices. The most common of Cuban fruits are:

<i>Achras zapota</i>	sapote
<i>Ananas sativus</i>	piña
<i>Annona cherimolia</i>	chirimoya
<i>A. muricata</i>	guanábana
<i>A. squamosa</i>	anón
<i>Averrhoa carambola</i>	carambola
<i>Carica papaya</i>	papaya
<i>Chrysobalanus icaco</i> *	icaco
<i>Chrysophyllum cainito</i> *	caimito
<i>Citrus aurantium</i>	naranja
<i>C. lima</i>	limón
<i>Eugenia jambs</i>	pomarrosa
<i>Mammea americana</i>	mamey

\* Native species.

<i>Mangifera indica</i>	mango
<i>Musa paradisiaca</i>	platano
<i>M. sapientum</i>	guineos
<i>Passiflora edulis</i>	granadilla
<i>Persea americana</i>	aquacate
<i>Punica granatum</i>	granada
<i>Psidium guajava*</i>	guayabo
<i>Tamarindus indica</i>	tamarindo

\* Native species.

When marking the introduced fruits in the above list the writer was deeply impressed with the truth of the economic principle that the number of introduced plants grown by a people is proportionate to their state of civilization. An asterisk was first placed opposite the names of the introduced plants. The number of asterisks increased with each re-checking of the list. Mr. Carabia added a few more, with the result that in the end but three fruits remained which were not so marked. So it was simpler to place an asterisk opposite the names of the native fruits. Of course, introduction here means into Cuba; many of the plants in the above list are of tropical American origin, such as the avocado, though numerous ones are from the Old World.

#### 7. COMMUNITIES AND GUILDS

Communities and guilds are small plant associations. They may have evolved independently, as has the guild of epiphytes, or they may be remnants of former and larger plant associations, in the latter case they are often the result of human activities. The vegetation forming a meadow is a guild or community of plants which has come into existence either by natural evolution, as is true of alpine meadows, or by the activities of man.

##### A. MEADOWS

Meadows are either natural park lands, or man-made pasture lands, distinguished from prairie and steppe by the presence of isolated trees, and from savana by a hygrophilous character. Size is usually not regarded as a distinguishing characteristic, yet meadows are smaller than either of their nearest grassland relatives.

Meadows occur most frequently in transitional areas, as hybrids of the two great plant associations, grassland and forest. Although meadows, as ordinarily encountered, are lands much modified by man through grazing, fertilizing, and mowing, yet there are natural meadows, park-like in their physiognomy, and readily differentiated from prairie, steppe, and savana. Fertility, moisture, size, grass, and scattered trees characterize the meadow. Several of these features in Cuban meadows are brought out by the presence of the island's most renowned plant, the royal palm, which is found only on fertile and moist soil (Figs. 42, 43).

In addition to the royal palm (*Roystonea regia*) two species of trees stand pre-eminent as the dominant arboreal plants of the meadows of Cuba; the bulky *Ceiba pentandra* (Fig. 43)—the Cubans pronounce it "sayba"—and the algarrobo, the great saman



FIG. 42. Royal palms in cane field.

or raintree, *Pithecellobium saman* (*Pithecellobium saman* or *Samanea saman*). All three species are widespread on Cuba's meadows, from western Pinar del Rio to eastern Oriente. They typify the meadows, fields, and gardens of Cuba, indeed of all the Caribbean. They are characteristic meadow trees, very rarely found on savana, the royal palm never.

Certain other trees, which have been considered elsewhere, are common on Cuban meadow land. Some are roadside trees, some invaders, and some escapes from the forest. Among these are *Gliricidia sepium*, called the living fence post, *Chlorophora tinctoria*, the widespread vagabond *Cecropia peltata*.



FIG. 43. A young *Ceiba pentandra*; royal palms on the right.

(Fig. 45), and the forest escape *Bursera simaruba*. The red-barked, gum-yielding tree, *Bursera simaruba*, to which this is the first reference, was formerly *B. gummifera*, and later became *Elaphrium simaruba*. Of these three names *B. simaruba* is now the accepted one. *B. glauca*, also written *Simaruba glauca*, is either a synonym or a distinct species; if the latter, it is a rare one. Though the writer's field notes contain references to each of these names including *B. glauca*, hereafter all of them will be referred to as *B. simaruba*.

The smaller, chiefly herbaceous plants of Cuba's meadows are quite similar throughout the island, for the meadows are all of arable, mostly calcareous soil. Some few plants of the ground cover are rather restricted, as is artemisa which is abundant in western Cuba. It is not the *Artemisia* of American deserts and Russian steppes, but *Ambrosia peruviana*, which, like *Artemisia*, is a medicinal composite. A collection made in a field near Artemisa in Habana Province will serve as an illustration of Cuba's meadow plants. One such gathering yielded the following:

<i>Croton sagraeanus</i>	Euphorbiac.
<i>Dicliptera assurgens</i>	Acanthac.
<i>Stigmaphyllon sagraeanum</i>	Malpighiac.
<i>Malvastrum coromandelianum</i>	Malvac.
<i>Anoda hastata</i>	Malvac.
<i>Namea jamaicense</i> var. <i>speciosum</i>	Hydrophyllac.
<i>Argemone mexicana</i>	Papaverac.
<i>Ipomoea ramoni</i>	Convolvulac.
<i>Cephaelanthus occidentalis</i>	Rubiac.
<i>Oxypolis bakeri</i>	Umbelliferae.
<i>Calotropis procera</i>	Aesclepiadac.
<i>Tridax procumbens</i>	Compos.
<i>Ambrosia peruviana</i>	Compos.
<i>Parthenium hysterophorus</i>	Compos.
<i>Eupatorium capillifolium</i>	Compos.
<i>Crotalaria retusa</i>	Leguminos.
<i>Desmodium incanum</i>	Leguminos.
<i>Sesbania grandiflora</i>	Leguminos.
<i>Distichlis spicata</i>	Graminac.

The meadow, as so far considered, may be regarded as a naturally evolved association of plants. In Cuba, there is little of such meadow for there is little untouched lowland. Quite other are the abandoned agricultural fields which soon become meadows. Invaders take possession, and the resulting plant community becomes a secondary development. The plants common to it are considered under "Invaders."

#### B. ROADSIDES

Planted roadside trees are quite likely to be introduced species because of their novelty or decorative value and because certain exotic plants thrive unusually well on foreign land. One does wonder, however, why it should be assumed that the Mediterranean legume, *Albizia lebbek*, tolerates Caribbean heat and aridity better than the tropical American "pepper" tree, *Schinus molle*, in view of the fact that the latter does so well on Mediterranean shores. Yet, so it is, or we imagine it; in any case we prefer the

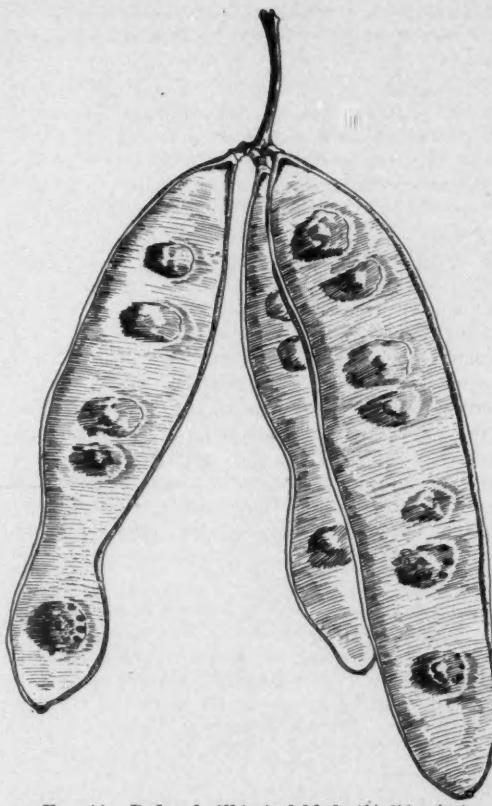


FIG. 44. PODS OF *ALBIZIA lebbek* (1/2 LIFE SIZE).

foreign plant to our native one, consequently the African lebbek tree is planted along Caribbean roadsides, and the American pepper tree lines the streets of Athens. *Albizia lebbek* is a very common tree throughout the populated regions of the American tropics. On St. Croix, among the Virgin Islands, the impression gained is that *A. lebbek* is the only tree on the island. When in fruit, its light brown, eight-inch pods are very conspicuous (Fig. 44).

The most abundant tree on Cuban roadsides is the small-leaved oriental fig, *Ficus benjamina*. It thrives well, forms a dense crown, and gives excellent shade; but Cuban botanists object to its extensive use maintaining that local trees will do as well for shade.

*Ficus benjamina* far outnumbers all other roadside figs, but *F. nitida* and *F. religiosa*, with its characteristic attenuated points, are quite frequently planted.

Not only introduced trees are very popular for planting. Quite frequent along many Caribbean roadsides is the sandbox tree (*Hura crepitans*), a particularly favored tree, for it makes excellent shade. Abundant also is majagua, *Hibiscus (Paritium) tiliaceum*. Less often planted is the mimosaceous *Enterolobium cyclocarpum*, called ear-tree, also orejo de judío, that is to say, "ear of the Jew." The

Guatemalan name is guanacaste; the tree grows best in that country, where it forms a magnificent canopy.

Occasionally fruit trees dot, though they rarely line, a roadside. Among them the most common is the jobo or hog-plum (*Spondias mombin*). Of native plants, a very characteristic one on Cuban roadsides is the royal palm (*Roystonea regia*) but it is planted for artistic effect only for it is not a good shade tree.

A very common sight in the American tropics is the "living fence." It occurs typically as sprouting fence posts set out as saplings and allowed to mature into trunks sufficiently substantial to carry a wire. The most common of these living fence posts is the legume *Gliricidia sepium*, though *Jatropha curcas* is frequently used for this purpose in Cuba.

Other types of living fences are hedges which turn cattle. They are commonly made of the bromeliad, *Bromelia pinguin* (Fig. 59), the liliaceous *Yucca aloifolia*, or the columnar cactus, *Cephalocereus*. The last often attains a startling height. Holdridge reports a 40-foot organ-pipe cactus hedge in Haiti.

#### C. REMNANTS

There are still existent in Cuba remnants of former lowland forests which contain reliques of what were once a flourishing vegetation. Such a remnant is the widespread almacigo (*Bursera simaruba*), a tree with smooth, red bark and a prolific yield of aromatic gum. Though common in Cuba as an isolated tree, in Haiti it occurs in nearly pure stands in lowland woods.

Often a tree remnant persists because it has been protected for its economical value. Large stands of valuable trees occasionally occur in the American tropics because they were left standing when their companions, in what was a mixed forest, were felled. The Indians preserved them for lumber or food. One such tree in Yucatan is *Achras zapota*, a lasting lumber tree. Another in Cuba is *Guazuma tomentosa*, a valuable forage tree when pasture fails.

Other reliques of former forests now common as individuals on meadows and rich savanas in Cuba are *Gliricidia sepium*, *Cecropia peltata*, *Chlorophora tinctoria*, and the calabash tree *Crescentia cujete*.

Tree remnants of former lowland Cuban forests include:

- Guazuma tomentosa*
- Bursera gummosa*
- Gliricidia sepium*
- Chlorophora tinctoria*
- Crescentia cujete*
- Cecropia peltata*
- Hibiscus tiliaceus*
- Swietenia mahagoni*
- Chrysophyllum oliviforme*
- Cedrela odorata*
- Guaiacum officinale*
- Jatropha curcas*
- Gilbertia arborea*
- Urera baccifera*

#### D. INVADERS

A consideration of invaders is of importance because of its bearing on the future plant life of a community. Invaders are pioneers and as such enter new, abandoned, or deforested land. They influence the composition of the soil, the extent of shade, and in other ways determine the habitat of plants which are to follow. Pioneers are among the most adaptable of plants. They invade and thrive on nearly all abandoned lands, but are likely to succumb later in the face of competition. In the former respect they are vigorous, in the latter they are feeble. Invaders in general survive only if and when they are pioneers.

The number of invaders on any given land is gradually reduced as other plants take hold, and continues to decrease until the invaders are eliminated. Invaders thus appear to be senescent species, but actually they are not, or only temporarily so, for they are rejuvenated by new habitats.

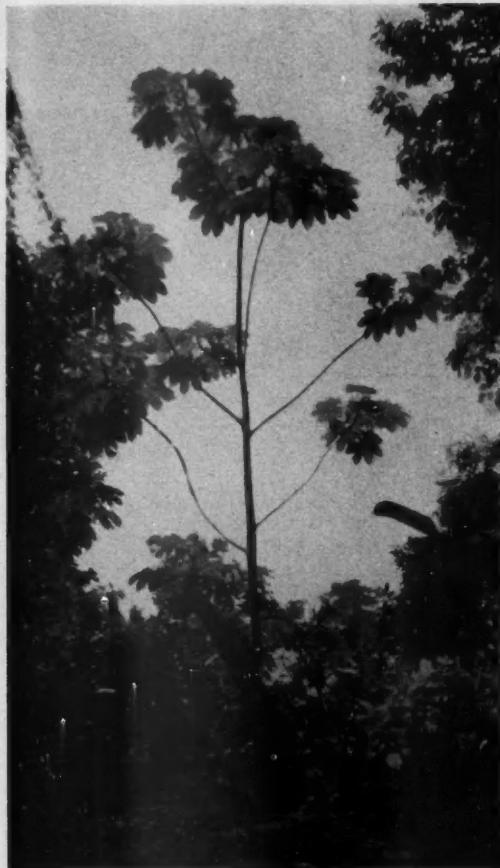
That invaders constitute a distinct ecological group is indicated by their abundance on recently abandoned lands in comparison with the sparsity of other species there. Furthermore, that the capacity of invaders to take hold of new land is a distinct physiological quality is shown by two such plants as *Ginkgo* and *Ailanthus*. Both are orientals, introduced into North America. *Ailanthus* has spread far and fast, whereas *Ginkgo* has given no evidence whatever of spontaneous germination. This brings up the question whether or not an invader shall be regarded only as an immigrant, as is *Ailanthus*. The writer does not think so. The plants which repopulated Krakatoa came from old vegetation on nearby land; they were invaders but they were also native species. Weeds are common invaders and, to be sure, are frequently immigrants from foreign lands but they can as well be native vagrants.

The greatest of all arborescent invaders on abandoned lands in the American tropics is the trumpet-tree (*Cecropia peltata*), called yagrumo in Cuba. It is the "tree-weed" of Caribbean lands (Fig. 45). *Cecropia* lacks one important qualification of invaders, that of wind resistance; and new territory is usually exposed ground. *Cecropia* has frail wood; still, it survives in open areas, though it rarely attains a large girth there.

*Cecropia* is always the first tree to enter abandoned coffee fields. The glistening, silvery under surface of its leaves, when blown back by a breeze, makes it a very conspicuous feature of the landscape.

*Comocladia* (Fig. 16) is a common invader of abandoned Cuban fields; its namesake, *Brunellia comocladifolia*, is also among the first woody plants to take possession of burned over areas.

If invaders are to be regarded as foreign immigrants only, then for Cuba the one great invader is the legume *Dichrostachys nutans*, called marabú, an introduction from South Africa. It is the most tenacious and prolific of all shrubby weeds in Cuba, forming vast thickets.

FIG. 45. *Cecropia peltata*.

The climatic and edaphic factors which determine the success of an invader are numerous; among them are wind, sun, acidity, and depletion in soil nutrients. Abandoned ground is frequently acid, though more often merely poor in nutrients. Shade is an important factor in the growth of seedlings. Many plants require it in order to get a successful start, and so, before they can make a beginning they must wait until more hardy pioneers have developed and formed shade.

The foregoing account is a very brief one for a subject of so much importance as the beginning of new vegetation on virgin ground. A classical study of this sort is that made on Krakatoa, an island denuded by volcanic eruption. A similar but more restricted study made in the American tropics is that by Johnson (1927). It deals with a Jamaican valley which had been completely stripped of vegetation by a heavy flood.

#### E. LAGOONS

The fresh-water plant life of Cuba centers in the island's largest lagoon, Ariguanabo, west of Habana.

The most abundant of the aquatics here is *Nelumbo pentapetalum*. But it is another which deserves first place among all tropical American aquatic plants, the floating and brilliantly flowered water-hyacinth, *Eichhornia crassipes*, widely spread from Florida to northern South America. With it occurs *E. azurea*.

Among the aquatics and sub-aquatics of Ariguanabo are *Nymphaea ampla*, *Nuphar advena* (*Nymphaea advena*), *N. odorata*, *Nelumbo luteum*, *Utricularia foliosa*, *Ceratophyllum demersum*, *Sesbania sesban*, *Pistia stratiotes*, and *Limnanthes grayana*. Near the water's edge are *Scirpus*, *Typha domingensis*, the legume *Cephalanthus occidentalis*, and *Salix occidentalis*. The last grows profusely on the borders of Cuban lagoons which are the southern limit for the species.

#### F. EPIPHYTES

Were one asked to select that plant community, or guild, which more than any other characterizes the vegetation of the tropics, it would certainly be the epiphytes. Cuba's epiphytic vegetation is rich. The writer has no exact counting for Cuba, but in order to give some idea of the prolific epiphytic plant life of tropical America, reference is made to a count in Jamaica where one limb yielded 52 species of plants. Epiphytes are more numerous and varied at higher altitudes because of greater humidity there, but the lowland epiphytic growth is not meager. Indeed, even in arid country, in a coastal thicket, an occasional thriving colony of epiphytes occurs. The character of epiphytes in arid regions indicates their xerophytic character. They are small with rather tightly compressed leaves. Examples of this among Cuba's epiphytic vegetation are the small *Tillandsia circinnata* (Fig. 15) and the still smaller *T. pruinosa* (Fig. 38).

The following are among Cuba's most abundant epiphytes:

BROMELIADS	<i>Philodendron lacerum</i> * <i>P. krebsii</i> ( <i>P. wrightii</i> )*
<i>Tillandsia recurvata</i>	
<i>T. balbisiana</i>	OTHERS
<i>T. polystachya</i>	<i>Marcgravia umbellata</i> * <i>Peperomia</i> spp. <i>Clusia rosea</i> *
<i>T. fasciata</i>	
<i>T. valenzuelana</i>	
<i>T. festucoides</i>	
<i>T. utriculata</i>	
<i>T. usneoides</i>	FERNS
<i>T. paniculata</i>	<i>Dryopteris</i>
<i>T. aloifolia</i>	<i>Polypodium</i>
<i>T. circinnata</i>	<i>Hymenophyllum</i>
<i>Aechmea nudicaulis</i>	<i>Trichomanes</i>
<i>Hohenbergia penduliflora</i>	<i>Adiantum</i>
<i>Vriessia ringens</i>	<i>Odontosoria</i>
<i>V. sanguinolenta</i>	<i>Oleandra</i>
<i>Guzmania monostachya</i>	<i>Elaphoglossum</i>
ARACEAE	CACTI
<i>Anthurium recusatum</i> *	<i>Rhipsalis cassutha</i>
<i>A. gymnonopus</i> *	<i>Selenicereus grandiflorus</i> *

\* Semi-epiphytes.

Certain epiphytic aroids are as common on rocks as on limbs, often more so, especially in semi-xerophytic, high-altitude fields. Such plants are still epiphytes, physiologically considered, but may be classed ecologically as lithophytes or saxicolous plants. Two such common in Cuba are the closely related *Aechmea nudicaulis* and *Hohenbergia penduliflora*.

There are also a number of pseudo-epiphytes which start their life epiphytically and often long remain so, but ultimately they get their air roots established in the soil and so become terrestrial. Among these pseudo-epiphytes are: *Anthurium recusatum*, *A. gymnopus*, *Philodendron lacerum*, *P. krebsii*, *Marcgravia umbellata*, *Clusia rosea* and *Selenicereus grandiflorus*.

#### 8. FORESTS

##### A. BARACOA

In traveling the Central Road from Pinar del Rio to Santiago, one would not say that Cuba is a land of forests. Savana and pasture are all that are visible except for a few scattered trees. But forests there are and magnificent ones too, indeed they are among the finest in the American tropics. Among the most valued trees are the jígue or sabicu (*Lysiloma sabicu*), mahogany (*Swietenia mahagoni*), guajacan or lignum vitae (*Guaiacum officinale*), mahagua (*Hibiscus tiliaceus*), granadillo or the West Indian ebony (*Brya ebenus*), agua baria (*Cordia gerascanthus*), ocoje (*Calophyllum antillanum*), acana (*Achras dissecata*), and caigarán (*Hymenaea courbaril*).

Oriente is Cuba's forested province, though there are some good woods on the slopes of the Trinidad Mountains in southern Santa Clara. The finest of the great forests are on the Baracoa Mountains in northern Oriente and on the Sierra Maestra in southern Oriente. Rather than attempt to cover the whole—a difficult task, for no botanist has as yet sufficient data—it will be better to center attention on one forest and study it in detail, with, however, brief references to several other forested regions. Therefore, the forests on the southern slopes of Pico Turquino will be treated in detail and short lists will be given of forest plants occurring in northern Oriente and southern Santa Clara provinces.

One thinks of Oriente as the humid part of Cuba, yet, as shown by precipitation data (Fig. 5), this is true only in a sense. Oriente is humid, but as much because of vegetation as rainfall. The character of plant life reflects this, and nowhere more so than at Baracoa where the vegetation is luxuriant.

The richness of vegetation in the Baracoa area is depicted by its fertile meadows and cultivated fields. There is no finer journey in all the American tropics than the several hours' ride between Baracoa and Mata. The scenery is exquisite, the vegetation luscious. One is left with two vivid impressions, great fertility and abundant moisture. Royal palms, indicators of good soil, are prolific. Coconuts, bananas,

cacao, and, on the higher slopes, coffee are extensively grown.

Beyond Mata is the renowned Gorge of the Yumuri (Fig. 46), one of the most picturesque canyons in



FIG. 46. Gorge of the Rio Yumuri.

Cuba, if not the only great one, for Cuba's rivers are few and short. Plant life is rich in the Gorge of the Yumuri. Outstanding plants are: *Rhytidophyllum tomentosum*, *Anastraphia ilicifolia*, *Legreliana*, and *Agave*.

Three other plants, common in humid agricultural regions, are the renowned trio of soft-wooded trees: *Cecropia peltata*, *Didymopanax morototoni*, and *Ochroma pyramidalis*. The most common among them is Cecropia, readily distinguished by its slender and ungainly form and its large palmate leaves (Fig. 45) with their silvery under surface. The second member of the trio, *Didymopanax*, is the matchwood tree. Its nine to eleven fingered leaves (Fig. 47) and tufted crown are readily noted. The third of these tropical American trees with feather-weight wood is *Ochroma pyramidalis*, or balsa wood, with large cordate leaves; it, too, is present in humid Oriente.

The following plants were noted in the vicinity of Baracoa:

FERNS	<i>Brya ebenus</i>
<i>Asplenium dentatum</i>	<i>Lysiloma bahamensis</i>
<i>Polypodium vezatum</i>	<i>Peltophorum adnatum</i>
<i>P. phyllitidis</i>	<i>Pithecellobium saman</i>
<i>Adiantum tenerum</i>	<i>Amrys diatrypa</i>
<i>Tectaria heracleifolia</i>	<i>Glycosmis pentaphylla</i>
<i>T. martinicensis</i>	<i>Spathelia vernicosa</i>
<i>Pityrogramma calomelanos</i>	<i>Stigmaphyllon lineare</i>
<i>Cyclopeltis semicordata</i>	<i>Gymnanthes recurva</i>
<i>Pteris longifolia</i>	<i>Orbicularia scopulorum</i>
<i>Sphenomeris clavata</i>	<i>Metopium venosum</i>
<i>Nephrolepis rivularis</i>	<i>Begonia wrightiana</i>
SEED PLANTS	<i>Ginoria glabra</i>
<i>Erágrostis hypnoides</i>	<i>Eugenia</i> sp.
<i>Cyperus ligularis</i>	<i>Pachyanthus mayarensis</i>
<i>Pseudolmedia spuria</i>	<i>Jacquinia aculeata</i>
<i>Ficus eggersii</i>	<i>Chrysophyllum argenteum</i>
<i>Neea theifera</i>	<i>Bourreria</i> sp.
<i>Capparis ferruginea</i>	<i>Cestrum daphnoides</i>
<i>Albizia cubana</i>	<i>Rondeletia</i> sp.
	<i>Guettarda elliptica</i>

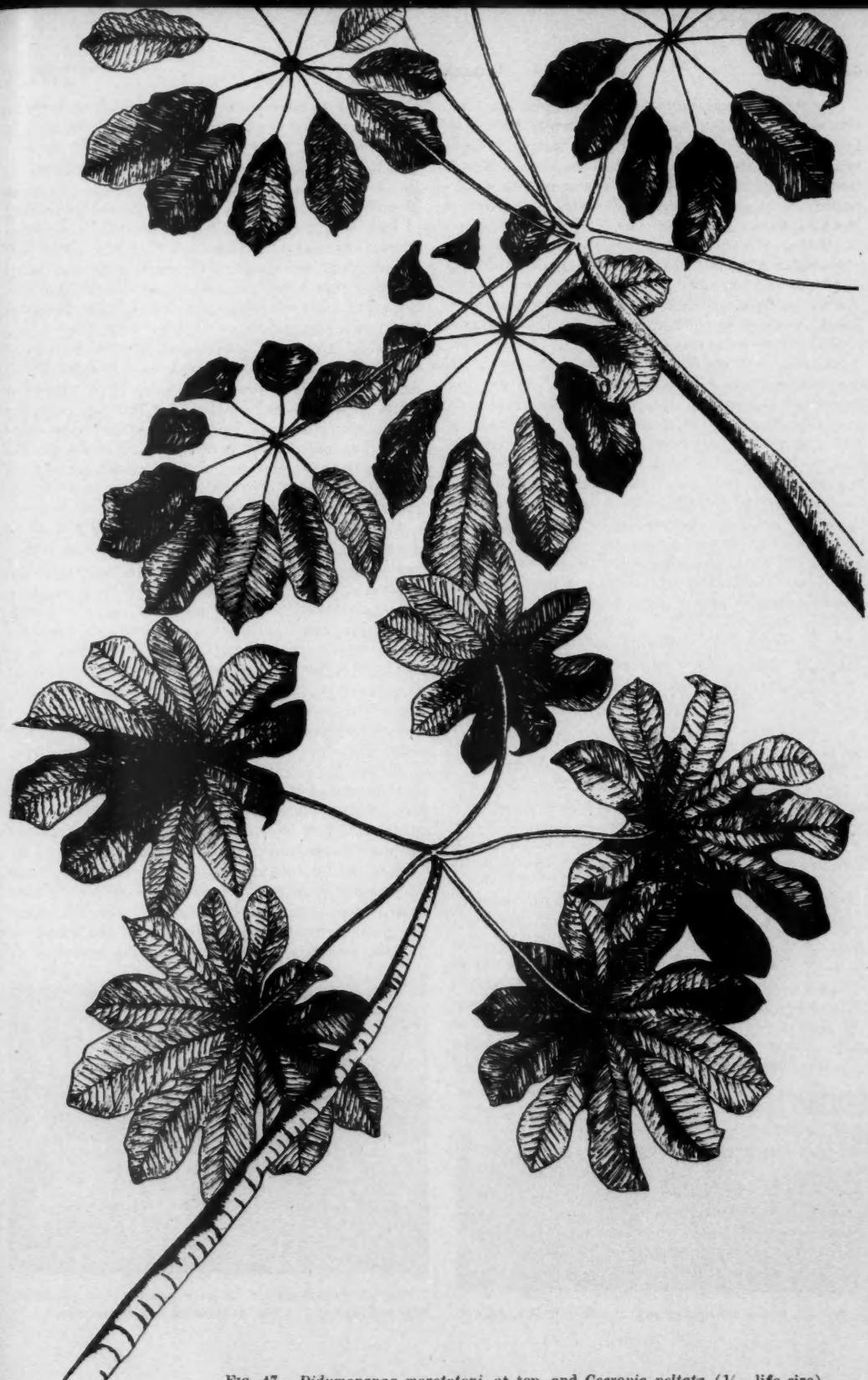


FIG. 47. *Didymopanax morototoni*, at top, and *Cecropia peltata* ( $\frac{1}{12}$  life size).

Among the foregoing plants several are distinctive. One of these, *Spathelia*, has been mentioned (Fig. 1). Rarer still is the American *Albizia*, a genus better known as the much planted African lebbek tree. Here it is the endemic *Albizia cubana*, occurring only in the lowland forests of the Baracoa Mountains near Batabano.

Another unusual plant in the Baracoa area is the arborescent *Pereskia cubensis*, which grows sparingly in the Oriente of Cuba. It is viciously armed with thorns. A relative of it, *Pereskia grandifolia*, from South America is much cultivated in Cuba because of its attractive flowers.

Slightly west of Baracoa is Moa, on the slopes of the northwestern Oriente mountains. In the pine forests of this region Marie-Victorin made the remarkable discovery of a new species of *Dracaena*. This historic genus is best known as *D. draco* in the Canary Islands. Heretofore, it has been known in the new world only as *D. americana*. It grows in Central America. Marie-Victorin has named the new species *D. cubensis*. It is a slender plant with a tuft of leaves at the top of a very tall stem.

Marie-Victorin gives the following as associates of *D. cubensis* in the Moa area: *Pinus cubensis*, *Bactris cubensis*, *Coccothrinax yuraguana* var. *orientalis*, *Cyathea aranosa*, *Lyonia macrophylla*, *Coccoloba shaferi*, *Hemocharis curtyana*, *Svenhedinia minor*, *Buxus marginalis*, *Poincianella* sp., *Guettarda crassipes*, *Caseria ilicoides*, *C. aquifolia*, *Anastraphia recurva*, and *Shaferia platyphylla*.

#### B. PICO TURQUINO

The forests of Pico Turquino are an integral unit in the vegetation of the mountain. The writer will discuss them as part of an account of the plant life of the mountain as a whole, but he must of necessity restrict his description to the southern slopes of Turquino. The northern side has been described by León, Ekman, et al. (1923).

Pico Turquino, the "turquoise" mountain, is at the western end of the Sierra Maestra Range which extends from Santiago de Cuba to Cape Cruz, a distance of 100 miles. Turquino is 63 miles from Santiago. The Sierra Maestra consist of a central ridge running east and west, parallel to the coast, with numerous spurs putting out to the north and south. There are several prominent peaks, Turquino being the highest among them, and the highest in all



FIG. 48. Pico Turquino and the Sierra Maestra.

Cuba. Its altitude is variously estimated at 6,300 to 7,200 feet. The Hydrographic Office now puts it at 6,560 feet.

The height of Turquino gives little indication of the magnificence of the mountain and its range. Mountains of twice this altitude usually gain much of their height from the elevation of the surrounding country, whereas the ascent of Turquino starts immediately at the shore. The entire elevation is attained within a distance of 5 miles from the coast; the more southerly peaks are but 4 miles from the sea.

Viewed from the Caribbean the Sierra Maestra present a superb spectacle with their wooded slopes descending close to the water's edge (Fig. 48). The entire region is heavily forested and but sparsely inhabited. The peak has been frequently ascended from the south, but only rarely by botanists, for the journey is a severe one with no well-marked trail. The ascent is arduous but not difficult for the experienced climber.

As Cuba's highest land, Turquino holds a place of distinction in the Antillean Archipelago. It is also one of the least visited of West Indian mountains because of its isolation. But its chief claim to honor lies in the fact that it is the summit of an exceedingly great and precipitous declivity; it caps the incline which starts 6 miles below at the bottom of the Bartlett Deep. This tremendous height, from the ocean floor at 3,000 fathoms to the peak of Turquino, a total of more than 28,000 feet, is attained within a distance of but 6 miles, thus producing a grade of about 45°.

At the foot of Pico Turquino, on the shores of the cove Bella Pluma, resides Juan Diaz (Fig. 49). He and his unnumbered family are the only residents on the coast at this point. Juan is the recognized guide for those who ascend Turquino from the south.

With the over-night sea journey from Santiago de Cuba accomplished—it is made in a hired or a chance fishing sloop—arrangements for the mountain journey must be made with Juan, and on the following day the ascent is begun. One allows a minimum of



FIG. 49. The home of Juan Diaz; note that the house wall is made of the leaf sheaths of the royal palm.

two days for the ascent and one for the descent, but when done in this short time the trip proves to be very tiring.

The vegetation of Pico Turquino is divisible into several altitudinal zones, as is plant life on mountains in general, especially in the tropics. When the mountain rises directly from the coast, it will harbor at least three main types of vegetation, grouped into zones or belts around the mountain side: these are the coastal belt, which consists usually of herbs and tree-shrubs; the central belt, which is forest; and the alpine belt, which is meadow or thicket. If the mountain is high, the major zones may be further subdivided; thus, the forest is divisible into a lower humid zone of large trees, and an upper, drier zone of small trees; and the alpine region may be divided into a subalpine association of high grass, and an alpine meadow of short grass. On the summit of tropical mountains there may also be savana, rocky paramo, or alpine thicket. Further subdivision will depend upon altitude, topography, geographic position, and declivity.

The mountain which is a perfect cone will have sharply differentiated altitudinal zones whereas a mountain eroded into deep valleys and ridges will not have clear-cut vegetational associations. A mountain which first attains great altitude many miles from shore, will have a broad coastal belt, a "littoral," with strand, desert, and thicket, whereas one rising directly from the shore with a rapid ascent will lack these familiar coastal associations. Pico Turquino has five well-marked, major, floristic zones, but they are not sharply differentiated as on a better-shaped mountain, such as Pangerango in Java, for Pangerango is a perfect cone and Turquino is much eroded with deep valleys (Fig. 51). On the other hand, Turquino has the advantage of rising directly out of the sea, whereas Pangerango rises from an inland plateau. The former conditions gives a more dramatic picture of the altitudinal distribution of plant life.

The plant zones on a mountain side may be described in terms of vegetation, geophysical characters, or climatic factors. Horizontal plant zones on the earth's surface, from north to south, are determined by gradations in temperature, or from east to west by moisture. The vegetation of North America illustrates this. Altitudinal zones are determined by both temperature and moisture.

Though temperature and moisture are primarily responsible for the zonation of plant life on mountain sides, soil, light, and wind play their part. The influence of wind is two-fold; it exerts a purely mechanical influence on plants, shaping them, and it has as well a drying effect. Light influences plant distribution in the tropics but little, though it must affect some activities such as time of flowering. Soil is either a local factor, or it may operate on a large scale. Pines and oaks are typically highland trees in the tropics, yet they often descend to the coast, as in Guatemala, following a granitic ridge

the entire way. The same situation exists to a lesser degree on Pico Turquino.

In spite of variations, it may be said that altitudinal zones of plant life show extraordinary uniformity wherever found. Local differences exist, thus, the coast may be wet or dry, and the alpine area be a meadow or a thicket; but, in the main, the vegetation on tropical mountains, from the Sierra Nevada of Colombia's Caribbean shores to the volcanoes of Java, may be divided into the following belts: 1. coastal flora, 2. lowland forest of large trees, 3. highland forest of small trees, 4. open herbaceous zone, 5. cloud forest, and 6. alpine meadow or thicket.

The naming of altitudinal zones rests on one of a number of qualities. Frequently moisture is chosen to characterize them. In terms of moisture the usual zonation on a tropical mountain becomes: 1. the xerophytic coastal zone, 2. the mesophytic forest zone, 3. the less moist, more open, highland forest. 4. the more arid, treeless, herbaceous zone, and 5. the semi-arid, alpine zone. Deviations are common. Exposure will, in the Antilles, make a north coast humid, with forest, and a south coast dry, with desert or thicket. A common variation is an alpine thicket instead of the customary meadow. Both Turquino in Cuba and Pangerango in Java have thickets at their summits.

A typical example of altitudinal zonations based on moisture is that given by Ciferri (l.c.) for Haiti, which, with slight variations, fits Pico Turquino in Cuba.

	Cuba
Mangrove forest.....	Strand
Hyperxerophytic forest.....	Swamp
Sub-hyperxerophytic forest.....	Desert
Savana.....	Thicket
Lagoon vegetation.....	Savana
Mesophytic forest.....	Lagoon
Hygrophytic forest.....	Lowland forest
Mountain forest.....	Alpine woods
Mountain savana.....	Alpine thicket
	Alpine fields

Variations, additions, and deletions will occur on every mountain. The south slope of Pico Turquino lacks the reeking wet woods of small, twisted, and moss-covered alpine trees better represented on the north slopes of Turquino. These cloud forests or "elfin woods" as Schimper called them, are found on most tropical mountains above 3,000 but best at 6,000 feet. In Cuba, the Baracoa and the Trinidad Mountains have wet alpine cloud forests. They are very well developed on Jamaica's Blue Mountains and the Pitons du Carbet of Martinique.

The vegetation on Pico Turquino will be discussed under 5 altitudinal zones: a. the coastal belt, b. the great forests, c. the high open forests, d. the subalpine herbaceous fields, and e. the alpine thicket.

#### a. The Coastal Belt

The coastal vegetation of Turquino is not wholly typical of the tropics, for the shore belt is too narrow

to give the customary associations. The great declivity, of which Turquino is the summit and the Bartlett Deep the base, continues its rapid ascent without interruption at the coast line. There is no flat lowland. Strand, desert, and thicket are poorly developed and swamp is wholly lacking. On sand patches here and there are *Ipomoea* and its companion *Canavalia*. *Coccoloba* forms the usual coastal wind-break, and back of it is a semi-xerophytic association of cacti and shrubs. The former include, *Dendrocereus nudiflorus*, the dwarf and spherical *Melocactus harlowii*, the rope-like epiphytic *Selenicereus*, and the ever-present *Opuntia*. The white flowered, sweet-scented, lirio de playa, *Plumeria alba*, is abundant.

The complete absence of the coconut palm is noticeable. The coconut is a domestic palm, and unless it is to some extent cared for it does not long survive. There is, however, a wild coastal palm, the small and slender *Coccothrinax gundlachii*, a reminder of the magnificent coastal palm at Maisi (Fig. 60), *C. alexandri*.

A shrubby growth just back of shore is all there is to represent the thicket so well developed in some localities where the coastal belt is broad.

#### b. The Great Forests

A mile from the sea one enters the lowland rain-forest (Fig. 50). It starts at about 300 feet altitude and continues up to 2,500 feet. Here are the great trees of Cuba. To single out dominants is impossible, for, as is true of all the tropics, the forest is a great mixture of species. One can only point to those which are somewhat more numerous than others. *Calophyllum antillanum* is perhaps the most common. Abundant are the familiar almácigo, *Bursera gum-mifera* (*B. simaruba*, *Elaphrium simaruba*), a common lowland Cuban tree, and the huge strangler, eopey, which is the guttiferous *Clusia rosea*, and jaquíey, *Ficus aurea*. Other large trees common in Turquino's southern forests are:

<i>Andira jamaicensis</i>	yabá	Leguminos.
<i>Guaicum sanctum</i>	guayacán blanco	Zygophyllac.
<i>Calophyllum antillanum</i>	ocuje	Guttiferae.



FIG. 50. Pico Turquino.

<i>Icica cubensis</i>	opal	Burserac.
<i>Sideroxylon foetidissimum</i>	jocuma	Sapotac.
<i>Dipholis gigantea</i>	juba	Sapotac.
<i>Carpodiptera cubensis</i>	majagua de Cuba	Tiliac.
<i>Cordia alliodora</i>	varia	Boraginac.
<i>Prockia crucis</i>	guasimilla	Tiliac.
<i>Tabebuia pentaphylla</i>	roble blanco	Bignoniac.
<i>Swietenia mahagoni</i>	caoba	Meliac.
<i>Prunus occidentalis</i>	almendro	Rosac.
<i>Cyrilla sp.</i>	barril	Cyrillac.

Among tropical vines there are always a few, known as water lianes, which bleed when cut. The common Cuban name for them is bejugo de parra, grape vine, or parra cimarrona (wild grape). The most common of the water lianes in the American tropics occurring on Pico Turquino, is *Vitis tiliifolia* (*V. caribaea*). Another liane of the Turquino forests which recalled to the writer his early years in Jamaica was the legume, *Entada scandens*; the Cubans call it boja.

Epiphytic plant life is not luxuriant, owing to insufficient moisture, but the narrow-leaved *Tillandsia* and the broad-leaved *Guzmania monostachia* are fairly common.

#### c. The High Open Forests

At Bobiney ("hog-wallow") one emerges from the lowland big-tree forest at an altitude of 3,000 feet, and enters the highland association of small trees. Many arborescent species here are the same as those in the lower forest, but the specimens are smaller. One is most impressed by the abundance of mela-stomes, a sierra palm, and another old friend from Jamaica, the scrambling bamboo, *Chusquea abietifolia*.

Open highland forests are the habitats of tree-ferns. They grow best in ravines where there is protection from the wind, cool air, moist soil, and good exposure to the sun. The tree-ferns on Pico Turquino are *Cyathea* and *Alsophila* species.

It has been argued that tree-ferns, and Pteridophytes in general, are "shade-loving" plants. This is certainly not true. The writer doubts if it is a correct interpretation of the habitat of many shade plants, in any case, not of ferns, for they do better in bright sunlight, provided that they have two other requirements which outweigh their preference for light. Ferns require a cool and moist environment, and this is usually to be had only in the shade. Tree-ferns are at their best when their roots are in cool, wet soil, and their crowns spread full to the sun.

A striking exception among ferns, not in their sun-loving propensities, but in their lack of resistance to arid habitats, is the widespread *Dieranopteris*. This wiry thicket-forming fern is found on hot, dry, open areas throughout tropical America, such as we are about to enter on leaving the moist mountain woods at Bobiney.

On the writer's earlier trips to the Caribbean, he knew the Jamaican *Dieranopteris* as *Gleichenia*, which

it had been called (Shreve 1914). According to current views the genus *Gleichenia* is restricted to a few species occurring only in Australia and adjacent regions. The American plants are referred to the segregate genus *Dicranopteris*. The species dichotoma belongs to the genus *Dicranopteris*. It is, however, an invalid name, the proper one being *Dicranopteris linearis*, and this species grows only in the Asiatic region. The Caribbean fern which we here have in mind is properly known as *Dicranopteris flexuosa*, of which synonyms are *Mertensia flexuosa*, and *Gleichenia flexuosa*.

Beyond Bobiney, at 3,250 feet, is Alto Cardero, and a little farther on, at 3,650 feet altitude, is La Cueva del Aura. The view in favorable weather is superb. One now realizes, if one has not already done so in ascending Turquino's slopes, that the declivity is exceedingly great (Fig. 51). The pan-



FIG. 51. The slopes of Pico Turquino.

orama reveals also how extensive and magnificent are Cuba's forests. That in which we are for the moment standing is an open forest at 3,000 to 4,000 feet altitude. It is dominated by *Hymenaea courbaril*, *Solonia reflexa* (*Walleniella cubana*), *Brunellia comocladifolia*, *Xolisma affinis*, *Dipholis cubensis*, *Tabebuia oligolepsis*, *Magnolia cubensis*, *Coccoloba monticola*, *Viburnum villosum*, *Garrya fadyenii*, *Taonabo leonis*, *Haemocharis angustifolia*, and *Vaccinium cubensis*.

Previous to emerging from the last stand of forest trees one meets with two conifers of unusual interest, a pine and a juniper. No pine was seen in the big-tree forest below; yet here, growing on an exposed ridge, is a large colony of *Pinus cubensis*. The underlying rock determines the presence of the pine here; the ridge is of granite. The second conifer is *Juniperus barbadensis*. It is abundant on the north slope of Turquino.

Another arborescent plant worthy of note at 3,000 feet on Turquino is the sierra palm, *Coccothrinax acunana*. It grows at higher altitudes than any other palm in Cuba, rivalling the renowned wax palms of Colombia. The last royal palm is found at 2,500 feet.

On departing from La Cueva one leaves the moist highland forest and enters an open and much exposed subalpine association of herbs, shrubs, and ferns, such as tolerate semi-arid conditions.

#### d. The Sub-Alpine Herbaceous Fields

In general, the summit of temperate mountains, from the Pyrenees to the Caucasus, is divided into a subalpine field of high grass and an alpine meadow of short grass. With the grass are herbaceous plants with conspicuous flowers. The subalpine belt, when at its best, presents one of the greatest flower displays which Nature has to offer. Especially abundant in most tropical subalpine fields are *Veronica*, *Clematis*, *Habenaria*, *Lantana*, *Begonia*, *Eupatorium*, *Lobelia*, *Hypericum*, and *Epilobium*, species of each of which are on Pico Turquino, in the Swiss Alps, and the Russian Caucasus. Even more surprising is it to find a species on a tropical mountain summit which one has collected north of the arctic circle. Such was the case with *Epilobium angustifolium*. It grows on Cuban mountains and in Russian Lapland.

Ferns are numerous on Cuba's mountains, especially the xerophytic *Dicranopteris flexuosa*. Present also are *Pteridium aquilinum*, *Polypodium*, *Diplazium*, *Adiantum*, and *Elaphoglossum*. The tree-ferns of Cuba include *Cyathea arborea*, *C. cubensis*, *C. insignis*, and *Alsophila aspera*.

The semi-arid character of the open subalpine formation on Pico Turquino is shown by the presence of *Agaves* clinging to precipitous crags (Fig. 52).

As the aridity is not extreme, epiphytic Bromeliads are numerous. *Tillandsias* and *Hohenbergias* are perched on every available stone.

#### e. The Alpine Thicket

The summit of Pico Turquino is credited with an altitude of 6,580 feet. This is not high enough for an alpine meadow in the tropics; its place on Turquino is taken by an alpine thicket. Alpine thickets have been referred to but little owing to their absence on temperate mountains and the paucity of ecological studies in the tropics, but they are very characteristic of mountain tops around the equator. The summit of Mt. Pangerango in Java is a thicket of *Vaccinium*, *Rubus*, and like shrubs.

The thicket which caps Turquino is a tall one, the slender trees averaging 12 to 15 feet in height. The association is very dense, a machete being necessary to cut one's way through.

Where an alpine thicket is open, there occurs a mixture of low thicket and meadow plants. Such a conglomerate, ecologically similar to that on the summit of Turquino is found at sea level in many north temperate regions. Species will differ, but the genera are the same. From those collected on the summit of Turquino, it is possible to recognize any familiar northern meadow-thicket. Whether it is in New England, on the summit of Pangerango in Java, or of Turquino in Cuba, the genera are the same: *Vaccinium*, *Myrica*, *Viburnum*, *Smilax*, *Clematis*, *Rubus* —it is a novel experience to gather wild raspberries

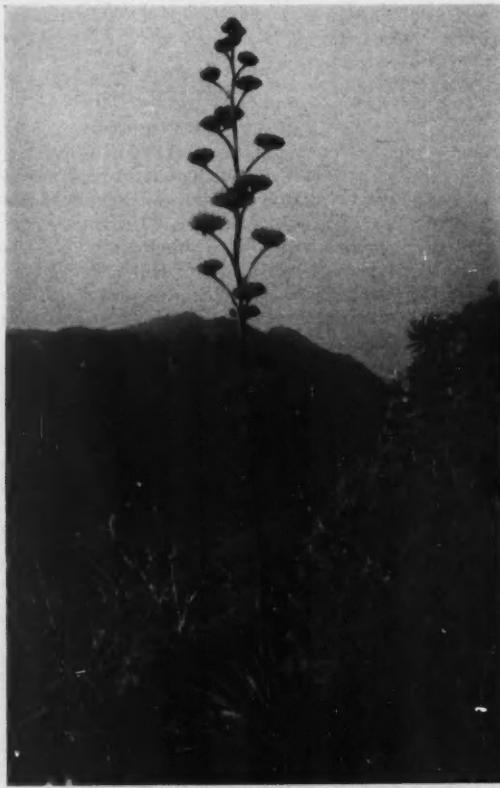


FIG. 52. *Agave* (probably *A. underwoodii*) in the open herbaceous zone at 4,000 feet, on Pico Turquino.

in the tropics—Hypericum, Vernonia, Pilea, Solanum, Eupatorium, Bidens, and the sedge Rynchospora.

Associated with these familiar northern genera on Turquino are many tropical ones, of which several are endemic. The most abundant tree is *Cyrilla racemiflora*, a genus and family (Cyrillaceae) which extends from the southeastern United States through the West Indies to northern South America. A typical, minute-leaved alpine thicket tree is *Rapanea microphylla* (Myrsinaceae). But that family of trees which, more than any other, is certain to be found high on tropical American mountains is the Melastomaceae, and among them the genus *Miconia*, predominates. The leaves of most melastomes are strikingly sculptured or embossed, thus aiding in identifying the family (Fig. 53).

Though the summit vegetation is a very heterogeneous mixture, several of the trees in the Turquino alpine thicket are far more abundant than others; one of these is *Haenianthus salicifolius*.

Orechids are well represented in the Turquino mountain thicket.

The following are the names of plants gathered on Pico Turquino, with some additions to the higher forest by G. C. Bueher of Santiago de Cuba. The

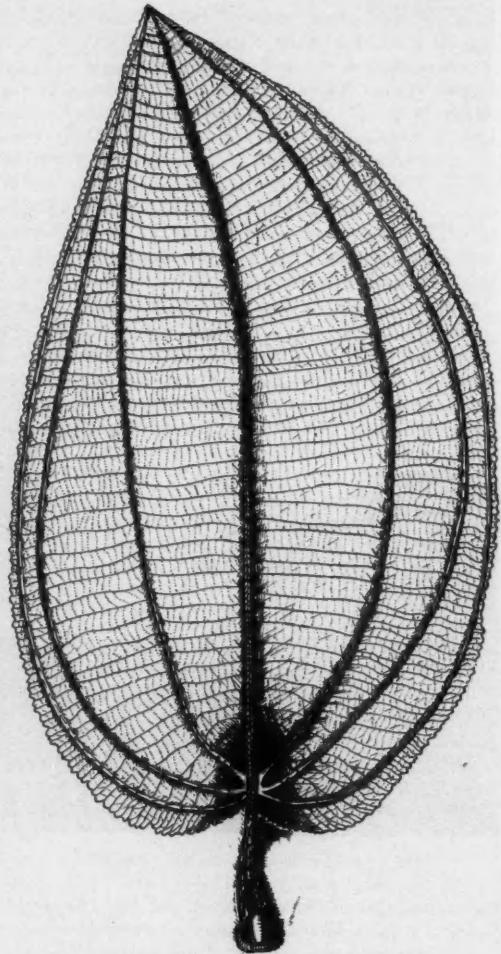


FIG. 53. *Miconia serrulata* (1/2 life size).

plants are arranged under the five zones into which the vegetation of Turquino has been divided: a. coast, b. great forest, c. highland forest, d. herbaceous zone, e. alpine thicket.

a. THE COAST—0 TO 100 FEET  
(Within one half mile of shore)

<i>Ipomoea pes-caprae</i>	<i>Opuntia dillenii</i>
<i>Canavalia maritima</i>	<i>Dendrocereus</i> sp.
<i>Peltophorum adnatum</i>	<i>Cephalocereus brooksianus</i>
<i>Funastrum clausum</i>	<i>Pavonia fruticosa</i>
<i>Commelinia elegans</i>	<i>Piper amalago</i>
<i>Isotoma longiflora</i>	<i>Sesuvium portulacastrum</i>
<i>Portulaca halimoides</i>	<i>Coccotrinax gundlachii</i>
<i>P. oleracea</i>	<i>Tephrosia cathartica</i>
<i>Plumeria obtusa</i>	<i>Echites umbellata</i>
<i>Passiflora suberosa</i>	<i>Solanum nigrum</i>
<i>Randia spinifex</i>	<i>Guilandina bouduc</i>
<i>Caesalpinia pauciflora</i>	<i>Capparis flexuosa</i>
<i>Rauwolfia canescens</i>	<i>Turnera ulmifolia</i>
<i>Stachytarpheta jamaicensis</i>	<i>Coccoloba uvifera</i>

## b. THE GREAT FOREST—500-2,500 FEET

<i>Andira jamaicensis</i>	<i>Bucida buceras</i>
<i>Guaiacum sanctum</i>	<i>Ecastaphyllum brownii</i>
<i>Calophyllum antillanum</i>	<i>Philodendron hederaceum</i>
<i>Bursera simaruba</i>	<i>Smilax sp.</i>
<i>Icica cubensis</i>	<i>Sapium jamaicense</i>
<i>Sideroxylon foetidissimum</i>	<i>Canavalia cubensis</i>
<i>Dipholis gigantea</i>	<i>Eranthemum nervosum</i>
<i>Pachira insignis</i>	<i>Guarea trichilioides</i>
<i>Carpodiptera cubensis</i>	<i>Ozandra laurifolia</i>
<i>Cordia aeliodora</i>	<i>Prunus occidentalis</i>
<i>Prockia crucis</i>	<i>Terminalia catappa</i>
<i>Tabebuia pentaphylla</i>	(introduced)
<i>Swietenia mahagoni</i>	<i>Epidendrum cochleatum</i>
<i>Clusia rosea</i>	<i>Calanthe mexicana</i>
<i>Ficus sp.</i>	

## c. THE HIGH OPEN FORESTS—2,500-4,000 FEET

<i>Symplocos leonis</i>	<i>Mouriria maestralis</i>
<i>Palicourea domingensis</i>	<i>Cytharexylum discolor</i>
<i>Gilibertia arborea</i>	<i>Lagettia sp.</i>
<i>Chiococca parvifolia</i>	<i>Magnolia cubensis</i>
<i>Solanum reflexa</i> ( <i>Walleniella cubana</i> )	<i>Coccobola monticola</i>
<i>Brunellia comocladifolia</i>	<i>Viburnum villosum</i>
<i>Cyrilla sp.</i>	<i>Garrya fadyenii</i>
<i>Freziera grisebachii</i>	<i>Symplocos leonis</i>
<i>Alchornea latifolia</i>	<i>Taonabo leonis</i>
<i>Torralbasia cuneifolia</i>	<i>Solanum pachyneurum</i>
<i>Xolisma affinis</i>	<i>Juniperus barbadensis</i>
<i>Dipholis cubensis</i>	<i>Cneorum trimerum</i>
<i>D. jubilla</i>	<i>Elaeagia cubensis</i>
<i>Tabebuia oligolepis</i>	<i>Haemocharis angustifolia</i>

## d. THE SUB-ALPINE HERBACEOUS FIELDS—4,000-6,000 FEET

<i>Malaxia domingensis</i>	<i>Lantanopsis hispidula</i>
<i>Pharus parvifolius</i>	<i>Callicarpa ferruginea</i>
<i>Phytolacca rivinoides</i>	<i>Catopsis nitida</i>
<i>Helianthus annuus</i>	<i>Pilea nudicaulis</i>
<i>Haenianthus grandifolius</i>	<i>P. miconiaeifolia</i>
<i>Agave underwoodii</i>	<i>Begonia cubensis</i>
<i>Chimarrachia cymosa</i>	<i>Ginoria glabra</i>
<i>Hillia tetandra</i>	<i>Bocconia frutescens</i>
<i>Palicourea alpina</i>	<i>Eupatorium sp.</i>
<i>Bidens reptans</i>	<i>Solanum sp.</i>
<i>Turnera ulmifolia</i>	<i>Rajania ovata</i>
<i>Linociera ligustrina</i>	

## e. THE ALPINE THICKET—6,000-6,500 FEET

<i>Ternstroemia parviflora</i>	<i>Eupatorium sp.</i>
<i>Persea anomala</i>	<i>Chimarrachia cymosa</i>
<i>Ocotea foeniculacea</i>	<i>Tillandsia didistichoides</i>
<i>Hedyosmum cubense</i>	<i>Lisanthus glandulosus</i>
<i>Psidium cacamminis</i>	<i>Rubus turquiniensis</i>
<i>Nectandra reticularis</i>	<i>Zeugites americana</i>
<i>Myrica cacamminis</i>	<i>Weinmannia pinnata</i>
<i>M. picardae</i>	<i>Salvia scopularum</i>
<i>Xolisma turquini</i>	<i>Callicarpa apiculata</i>
<i>Ilex berteroii</i>	<i>Peratanthe cubensis</i>
<i>Cyrilla racemiflora</i>	<i>Dendrophthora cupressoides</i>
<i>Ditremena ligustrina</i>	<i>Miconia nystromii</i>
<i>Cissus tuberculata</i>	<i>Haemocharis angustifolia</i>
<i>C. microcarpa</i>	<i>Peirania robiniaeifolia</i>
<i>Rynchospora polypyphylla</i>	<i>Elaeagia cubensis</i>
<i>Clematis dioica</i>	<i>Sapium sp.</i>
<i>Vernonia gnaphaliifolia</i>	<i>Cestrum turquinense</i>

## clematis dioica

<i>Bidens leucantha</i>	<i>Stelis ophioglossoides</i>
<i>B. brittonii</i>	<i>Leiphaimos aphylla</i>
<i>Borreria arboreascens</i>	<i>Iresine celosia</i>
<i>Brachymerium wrightii</i>	<i>Lisanthus glandulosus</i>
<i>Maytenus sp.</i>	<i>Hillia tetranda</i>
<i>Vaccinium cubense</i>	<i>Lobelia cacuminis</i>
<i>Pilea chamaedrys</i>	<i>Asplenium erosum</i>
<i>Lepanthes ovata</i>	<i>Marattia alata</i>
<i>Viburnum villosum</i>	<i>Plagiogyria semicordata</i>
<i>Peperomia tenella</i>	<i>Diplazium l'erminei</i>
<i>P. ekmani</i>	<i>Dicranopteris bifida</i>
<i>Haenianthus obovatus</i>	<i>Elaphoglossum firmum</i>
<i>H. salicifolius</i>	<i>Gymnogramma cubensis</i>
<i>Palicourea alpina</i>	<i>Odontosoria uncinella</i>
<i>Rapanea microphylla</i>	<i>Polypodium turquinum</i>
<i>Ditta myricoides</i>	<i>P. loricatum</i>
<i>Gesneria viridiiflora</i>	<i>P. asplenifolium</i>
<i>Dendrophthora myrtilloides</i>	<i>P. senile</i>
<i>Hypericum fasciculatum</i>	<i>P. lycopodioides</i>
<i>Mitracarpus sp.</i>	<i>Hymenophyllum fucoides</i>
<i>Chusquea abietifolia</i>	<i>H. polyanthos</i>
<i>Eurva sp.</i>	<i>Lycopodium pithyoides</i>
<i>Oncidium variegatum</i>	<i>L. clavatum</i>

## C. CLOUD FORESTS

The chief characteristics of cloud forests are their high humidity, their reeking wet covering of mosses, prolific epiphytic growth, and abundance of ferns, especially the filmy.

As cloud forests are not well developed on the south slopes of Pico Turquino—they are too dry—the forests on the Trinidad Mountains (Fig. 54) will be described as the Cuban example of a cloud forest. The trees there include: *Zanthoxylum*, with its colossal pseudo-thorns; *Gilibertia arborea*; *Clusia rosea*, found from sea coast to mountain top; *Ficus*, possibly *F. aurea* and *F. laevigata*; the robe, or rather one of them, *Tabebuia pentaphylla*; the widespread *Bursera simaruba*; the pomarosa, *Eugenia jambos*, with an edible, perfumed fruit; *Cecropia peltata*; the matchwood tree or yagrumo macho, *Didymopanax morototoni*; the juecaro, *Buchenavia capitata*; *Miconia* and other Melastomaceae; the jagua, *Genipa americana*; and the majagua, *Hibiscus tiliaceus*. Smaller plants include the herbs *Peperomia*, *Begonia*, and *Passiflora*, all three of which are abundant on mountains throughout the Caribbean; the epiphytic pendant *cactus*, *Rhipsalis*; several bromeliads, chiefly *Tillandsia tenuifolia* with grass-like leaves; numerous orchids including *Iochilus* and the tiny *Pleurothallis*; a woodland grass, *Pharus glaber*; and an abundance of ferns including the tree-ferns *Alsophila* and *Cyathea*, the terrestrial ferns *Tepteris*, *Dryopteris*, and *Asplenium*; the climbing *Struthiopteris* and *Lygodium*, the epiphytic *Polypodium phyllitidis* and *Pessopteris*, and the filmy ferns *Hymenophyllum* and *Trichomanes*, the last always conclusive evidence of high, wet, tropical mountain woods.

## 9. MAISI

Miasi is in a phytogeographic class by itself. It combines in one picture much of the diversity of



FIG. 54. The fertile slopes of the Trinidad Mountains; royal palms in the foreground.

Cuban vegetation, compactly arranged in a series of terraces. Each altitudinal zone is here sharply delimited by an escarpment.

Punta Maisi is the eastern tip of Cuba (Fig. 55). The town of the same name is on the north side of the hot coastal plain known as El Llano de Maisi which terminates the island. At the edge of the sea stands the Faro de Maisi, the beacon which directs ships through the Paso de los Vientos. This ocean passage between Cuba and Haiti is well named, for the winds there seem never to cease.

Miasi is a small village of some two hundred scattered houses. Accommodations are to be had by arrangement at the home of the lighthouse keeper, Alejandro Lopez, who, with his family of fifteen, welcomes one with the hospitality of a true Castellano.

The Llano de Maisi is the driest region on the



FIG. 55. The eastern tip of Cuba with its wind-blown hedge of seagrass.

island, often no rain falling from February to August, or even until October, though other parts of Oriente are very wet. The reason for this is the continuous wind which sweeps across the Straight between Haiti and Cuba. The moisture laden clouds pass over the flat plain without hindrance by mountain ranges.

The low coastal plain or Llano de Maisi is the first in a series of six major and numerous minor "mesas," "euestas," or terraces (Fig. 56). With each

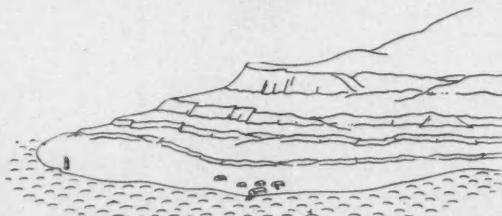


FIG. 56. The terraces at Maisi.

sudden rise in elevation, a new association of plants occurs which is more or less sharply differentiated from the adjoining ones. The floras of the separate terraces are distinctive, though some species occur at several levels, and one, *Clusia rosea*, is found from sea coast to mountain top. The Clusiads of Cuba have not all been named; the Maisi species may be *C. minor* or *C. teiastigma*. Elsewhere, as in the Trinidad Mountains of Cuba, in Haiti, and in Guadeloupe, *C. rosea* occurs from sea coast to mountain summit. Marie-Victorin and León picture it on the summit of la Loma del Gato in Cuba.

The journey from coast to mountain top at Maisi is some 15 miles long, and the rise 2,250 feet. Within this distance and elevation, the vegetation changes from a lowland xerophytic one to a high wet elfin forest. Nowhere else in the Caribbean area is there so fine and pronounced an example of an altitudinal change in vegetation within so short a distance as at Maisi.

Marine terraces characterize much of the coast of Oriente. At Maisi the mesas broaden and instead of following the coast cut across the tip of the island. The terraces are the result of faulting in late Pliocene or early Pleistocene, the main result of which was the formation of the great submerged scarp which forms the Bartlett Trough. The basal rocks, of complex metamorphic composition, are overlaid with Miocene marls and limestones which form the surface of the Maisi terraces of today.

#### A. THE LLANO DE MAISI

The first of the five mesas at Maisi, the Llano or plain at sea level, supports a most extraordinary association of plants. The psychological effect on the visitor is an indicator of the vegetation. The impression is a fearful and repellent one, for it seems impossible that human beings could long survive in so desolate a waste. But while repelling, it fascinates, and for the botanist it is a superb and little-touched collecting ground.

The coastal plain is of several parts, each distinct as to vegetational type. There are swamp, strand, hedge, desert, thicket, and palm savana.

Part of the Maisi coast, to the north, is swamp. It harbors three mangroves: *Rhizophora mangle*, *Conocarpus erecta*, and *Laguncularia racemosa*.

The remainder of the coast is strand. Nearest the water's edge are the woolly creeper *Ambrosia hispida*—its name indicates the pleasant, pungent odor of its leaves—and the little mat-forming *Heliotropium curassavicum*. Among grasses there are *Chloris* and *Sporobolus*, and with them the sedge *Cyperus*. The shrub *Tournefortia gnaphalodes* is abundant. The beach morning-glory, *Ipomoea pes-caprae*, is for some unknown reason absent.

Between strand and desert is a hedge of the sea-grape, *Coccoloba uvifera*. It forms a natural wind-break, itself well streamlined by the wind (Fig. 55). In its shelter grow a variety of small trees and shrubs, including *Catalpa punctata*, *Croton lucidus*, *C. stenophyllus*, *Cassia*, *Chrysobalanus icaco*, and *Capparis grisebachii*.

The central portion of the Maisi plain is a desert, such as is typical of all dry Caribbean coasts. It contains the expected cacti and microphyllous shrubs, all kept dwarfed by constant winds (Fig. 57). The cacti are *Cephalocereus*, *Dendrocereus*, *Lemaireocereus*, and *Melocactus*. Shrubs and small trees are numerous; the dominants are the two ulmaceous tree-shrubs *Erythroxylon* (Fig. 58) and *Phyllostylon* (Fig. 59). Both are microphyllous tree-shrubs and both when on an open desert assume the character-



FIG. 57. The Maisi desert; the wind-cropped mounds are of *Erythroxylon brevipes*, and the dwarf cacti are *Cephalocereus brookianus*.

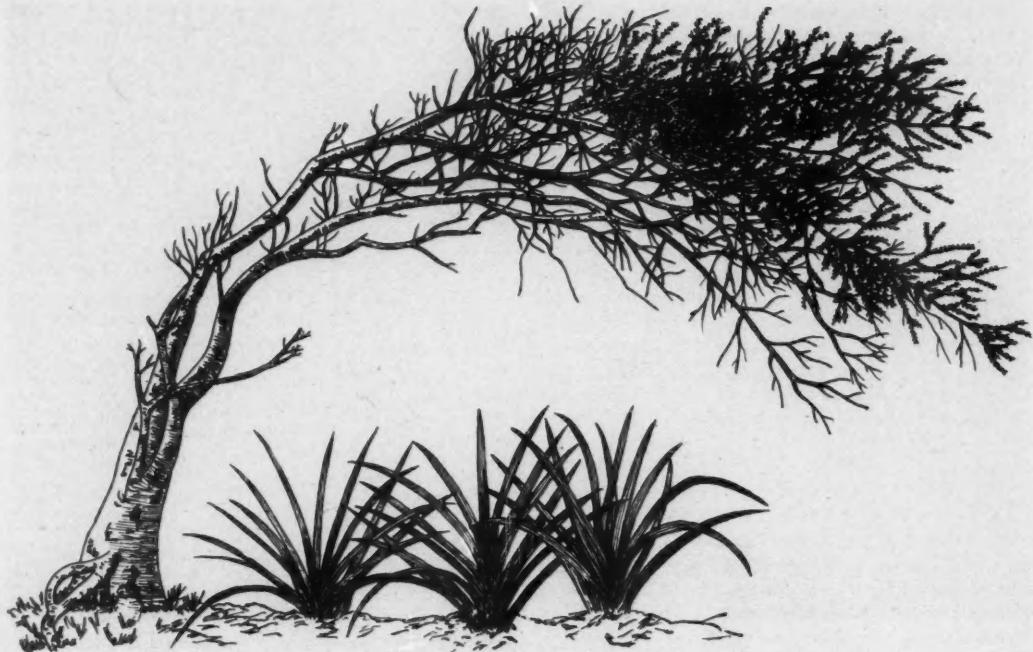
istic form of wind-cropped (Fig. 57) or wind-blown plants (Fig. 59).

Only recently has Maisi been thoroughly investigated botanically. In the past, L. H. Bailey collected palms there, and Ekman was, of course, there. Hermano León first visited Maisi with the writer in 1935, and has since made two more visits with Frère Marie-Victorin. It is, therefore, hardly to be expected that all species have been finally named. Among the uncertain plants are the two just mentioned. There are apparently several species of *Erythroxylon* in the Maisi desert and thicket. Hermano León and Frère Marie-Victorin adopted *E. brevipes* as the dominant species, but *E. minutifolium* may also be present. There is difficulty in regard to *Phyllostylon*; it may, for example, be an *Erythroxylon* gradually increasing in size as it grows farther and farther from the coast until it becomes erect. However, as this has not been definitely established, the writer has chosen to regard it as *Phyllostylon brasiliense*. This question will have to be answered by future botanists who visit Maisi.

The inner half of the Maisi plain is covered by a transitional association which is mostly thicket. It grades into the more compact thicket of the next mesa. The vegetation of the inner portion of the coastal plain is composed of a great variety of shrubs and small trees, legumes predominating; they include *Acacia spinosa*, *Pithecellobium hystrix*, *Caesalpinia bahamensis*, and a *Malpighia*. Present



FIG. 58. *Erythroxylon minutifolium*.

FIG. 59. The wind-blown *Phyllostylon brasiliense*, with *Bromelia pinguin* below.

also are *Urechites lutea*, *Cordia alliodora*, *Cochrorus hirsutus*, *Plumeria*, *Omphalea*, *Amyris*, *Pseudocarpidium*, *Hamelia*, *Lasioerotom*, and *Guajacum*.

A touch of color is given to the uniform gray of the plain by the pink flower of the herbaceous "vicaria," *Lochnera (Vinca) rosea*.

Nearby, the guide Prudencio Matos collected and Hermano León named a new "sabrosa" (*Jatropha*); it became *Cnidoscolus matosii*.

The last of the distinctive plant associations on the Maisi plain is a palm savana. Two palms characterize the association, a *Coccothrinax* and *Thrinax parviflora*.

Hermano León has recognized the Maisi *Coccothrinax* as a new species and named it *C. alexandri*. It is a striking palm, tall and slender, and occurs in considerable numbers, though restricted in distribution (Fig. 60).

#### B. EL CHIVO

The change in elevation from the coastal plain to the first terrace is slight and imperceptible in parts, but precipitous elsewhere, reaching a maximum of 250 feet over the sea. This, the first mesa above the Llano, is known as "El Chivo," literally "the goat," so-called from the great numbers of goats which formerly roamed there. Though the increase in altitude is barely perceptible in parts, from a distance the two zones, the Llano de Maisi and El Chivo, are distinguishable by their color, the gray of the shrubs and eacti of the plain contrasting with the brighter green of the trees of the upper

level. That one has entered a distinct association of plants is evident from the increased height of the plants and the addition of other species. The eacti develop into huge plants (Fig. 11) owing to protection from the winds which sweep the Llano. Abundant among them is *Dendrocereus nudiflorus* (Fig. 61).

The woody plants of El Chivo are more numerous, larger and more varied than on the coastal plain. New species include another *Erythroxylon*, *E. rotundifolium*, the "wild pine" *Bromelia pinguin* which is frequently planted as a hedge (Fig. 59), an *Exostemma*, a *Lysiloma*, and *cupey*, the gutti-

FIG. 60. *Coccothrinax alexandri* at Maisi.



FIG. 61. Detail of *Dendrocereus nudiflorus* on the arid Maisi plain; *Erythroxylon minutifolium* is in the left background.

ferous *Clusia rosea*. The legume *Lysiloma latisiliqua* is an interesting tree, widespread in Cuba. It outdoes the northern shag-bark hickory in the matter of a shaggy bark.

A prize on the Chivo is the palm, *Pseudophoenix sargentii* (Fig. 62). It is a relative of *P. vinifera*, the "lost palm" of Haiti, first known from the Bahamas, rediscovered by Ekman, and later found by David Fairchild on Saona Island, south of Santo Domingo. *Pseudophoenix vinifera* was long known to occur in Hispaniola as a source of palm wine, similar to the Areca palm which yields the "toddy" of Ceylon, but was not until recently found in Cuba.

Another rare plant on El Chivo is the eyad *Zamia*, possibly *Z. latifolia*.

An orchard of the cashew nut (*Anacardium occidentale*) still persists, the relic of an attempt at horticulture on El Chivo.

The elevation of El Chivo over the coastal plain is in parts insufficient to account for so great a change in flora, nor does the rainfall of the two areas differ much; there must be other causes. One of the lesser of these is the greater protection from wind which the upper terrace receives. Another factor is the substratum. Eroded limestone rock with pockets of soil forms the floor of El Chivo,



FIG. 62. The rare *Pseudophoenix* on the arid mesas of eastern Cuba.

whereas a fine limestone soil with humus brought down from above by flooded rivers, coats the plain. More significant still is the difference between the ages of the two regions. El Chivo is much older than the plain; the dividing line between the two was the former coast line of Cuba. Age has thus given the vegetation of El Chivo time in which to develop into a more mature association.

#### C. MESA DEL LINDERO

The second vegetational zone and its terrace ends abruptly at the base of high coral cliffs. Three to four hundred feet above is the Lindero, the "mesa del palo," or forested terrace. It is less distinctive than El Chivo below but has some characteristic species, notably *Oxandra lanceolata*, *Jacquinia aculeata*, *Exothea paniculata*, *Hamelia lutea*, *Cordia globosa*, *Trichachne insularis*, *Cupania glabra*, *Tecomia stans*, *Selenicereus urbanianus*, *Leptocereus maxoni*, *Acrocomia crispa*, and *Roystonea regia*.

## D. MESA DE LA YAGRUMA

The succeeding terrace or fourth zone is the "mesa de la Yagruma," 1,000 feet in altitude. It derives its name from Yagruma, *Cecropia peltata*, which is extraordinarily abundant here. Also present are *Alchornea latifolia*, *Nectandra coriacea*, *Oxandra laurifolia*, *Clusia rosea*, *Cedrela mexicana*, *Cordia gerascanthoides*, *Celtis trinervia*, *Passiflora multiflora*, and several species of *Ficus* including *F. aurea*.

## E. MESA DE MIRABEL

The next terrace or fifth zone is a minor one, the "mesa de Mirabel" with a vegetation derived from the two adjoining terraces. The mesa rises but 50 feet above the mesa de la Yagruma, and is, therefore, with difficulty distinguished from the adjoining terraces. It can, however, be characterized by two trees, one, *Victorinia regina*, commonly known as the sabrosa. This new species was split off from the better known sabrosas of the genus *Jatropha*. It is a euphorbiaceous tree of good size, and highly toxic.

The other endemic on the mesa de Mirabel is *Roystonea regia* var. *maisiana*. Both were named by Hermano León.

## F. LOS LLANOS

The last terrace proper, Los Llanos, is an extensive plateau some 1,500 to 1,600 feet in altitude. Here are great banana and coffee plantations. Areas not cleared contain many large trees, relics of a former virgin forest; among them are the juba, *Diphollis juba*, one of the mammoth trees of Cuba; the saman or rain tree, *Pithecellobium saman*, with its magnificent spread of crown; the cedro, *Cedrela mexicana*; the jobo or hog-plum, *Spondias mombin*; the giant figs, species of *Ficus*; the sabrosa, probably an endemic species of *Jatropha*; *Sterculia apetala*, a great tree in the American tropics; *Zanthoxylum*, a genus common to Cuba occurring here as *Z. martinicense* and *Z. elephantiasis*; *Cecropia peltata*; the espadera or matchwood tree, *Didymopanax morototoni* which is "yagruma macho" or the "male" *Cecropia* and a rival of *Cecropia* in lightness of wood; *Guarea trichilioides*, *Cupania americana*, *Alchornea latifolia*, *Misanthea triandra*, *Hufelandia pendula*; *Ocotea leucoxylon*; *Torrubia obtusata*; *Eugenia jambos*; *Citrus vulgaris*; *Urera maccifera*; *Bryum leoni*; *Philonotis tenella*; *Vitis caribaea*; *Psidium guajava*; *Tournefortia hirsuta*; *Pisonia aculeata*; *Ipomoea siderea*; *Bignonia gnaphalantha*; *Passiflora quadrangularis*; *Sapium jamaicense*; *Prunus occidentalis*; *Cupania americana*; and *Guazuma tomentosa*.

The royal palm reaches its greatest development at Los Llanos. It is scattered throughout the plantations and forests. There is considerable variation in its individuals which will probably result in the splitting off of two or more species. Since writing the above, Hermano León has isolated three species, *Roystonea violacea*, *R. lensis*, and *R. stellata*.

The "corojo," *Aerocoma*, a palm readily distinguished by its carrot-shaped trunk and the disheveled

appearance of its crown (Fig. 41), is here the newly described endemic species *A. pilosa* (León).

Greater moisture, a cooler temperature, a larger expanse of level ground, and the presence of agriculture, all contribute to a varied and more luxuriant vegetation at Los Llanos.

At the Fernandez plantation on Los Llanos, Cuban hospitality, perpetuated as a heritage from Spain, again manifests itself, and proves a comfort to the traveler in these little frequented parts. Horses may be obtained for the ascent to the summit of Vista Alegre.

## G. VISTA ALEGRE

No region is more familiar, more quickly characterized, and brings greater joy to the heart of the tropical plant explorer than a mountain cloud forest. The general appearance and make-up of these wet, high altitude forests are similar on all Caribbean mountains. The plant families, with the exception of a few endemics, are the same, the genera are similar, and many species are common to all "elfin woods" in their respective hemispheres. The experienced explorer jots down the dominant plants without raising his eyes from his note book and then looks about to see if he has recorded all genera that are there, and any that are not there. To prove the truth of this, we might make a list of high, humid, forest plants occurring in Jamaica and see how well the list holds for Vista Alegre of Oriente in Cuba; *Eugenia*, *Nectandra*, *Cecropia*, *Melastomaceae* including *Miconia*, *Clusia*, *Tillandsia*, *Gumania*, epiphytic orchids, the vine *Maregravia*, the pendant cactus *Rhipsalis*, *Alsophila*, *Cyathea*, *Polypodium*, *Nephrolepis*, and the filmy ferns, *Hymenophyllum* and *Trichomanes*. If to this list we now add a Sierra palm, which does not grow at high altitudes in Jamaica but is common to mountain forests in Haiti, Puerto Rico, Venezuela, and Colombia, we shall have a perfect listing of the dominant plants in the wet, alpine forests of Oriente, Cuba (Fig. 63).

The forests at Vista Alegre contain an unusual number of palms; they include the manaca palm, *Calyptronoma dulcis*, the boba or sierra palm, *Euterpe globosa*, and the pajuá palm, *Bactris plumeriana*. Ferns are abundant; among them being *Oleandra*, *Odontosoria*, and the rare *Olfersia cervina*.

The following are the representative plants of the terraces above Punta Maisi, arranged in the order of their altitudinal distribution:

## LLANO DE MAISI (Sea level)

Strand	Swamp
<i>Ambrosia hispida</i>	<i>Rhizophora mangle</i>
<i>Heliotropium curassavicum</i>	<i>Conocarpus erecta</i>
<i>Chloris petraea</i>	<i>Laguncularia racemosa</i>
<i>Sporobolus indicus</i>	Seagrape hedge
<i>Cyperus brunnescens</i>	<i>Coccocoba uvifera</i>
<i>Euphorbia buxifolia</i>	<i>Catalpa punctata</i>
<i>Tournefortia gnaphalodes</i>	<i>Croton lucidus</i>
	<i>C. stenophyllus</i>



FIG. 63. Alpine woods at Vista Alegre; upper left corner, *Guzmania monostachya*; upper right and lower left, *Philodendron*; central tree is *Didymopanax morototoni*.

*Cassia occidentalis*  
*Chrysobalanus icaco*  
*Capparis grisebachii*

*Cochrurus hirsutus*  
*Amyris balsamifera*  
*Pseudocarpidium shaferi*  
*Hamelia lutea*

## Desert

*Cephalocereus brooksianus*  
*Lemaireocereus hystrix*  
*Dendrocereus nudiflorus*  
*Opuntia dillenii*  
*Melocactus acunai*  
*Consolea macrantha*  
*Erythroxylon areolatum*  
*E. brevipes*  
*E. minutifolium*  
*Phyllostylon brasiliense*  
*Urechites lutea*  
*Cordia alliodora*

## Thicket

*Agave* sp.  
*Acacia spinosa*  
*Pithecellobium hystrix*  
*Caesalpinia bahamensis*  
*Malpighia* sp.  
*Plumeria obtusa*  
*Omphalea* sp.  
*Lasiocroton bahemensis*  
*Guayacum sanctum*  
*Ehretia tinifolia*  
*Lochnera rosea*  
*Thrinax parviflora*  
*Coccothrinax alexandri*  
*Cnidoscolus matosii*

## EL CHIVO (250 feet)

*Erythroxylon rotundifolium*

*Bromelia pinguin*  
*Clusia rosea*

*Pseudophoenix sargentii*  
*Malpighia* sp.  
*Simaruba* sp.  
*Exostemma spinosum*  
*E. caribaeum*  
*Guettarda* sp.  
*Randia sagrana*  
*Argemone mexicana*  
*Lysimoma bahamensis*  
*Chrysophyllum oliviforme*  
*Mimusops albescens*  
*Aristolochia* sp.  
*Hypelate trifoliata*  
*Serjania subdentata*  
*Anastraphia northropiana*  
*Buxus* sp.  
*Pitcairnia cubensis*  
*Tillandsia recurvata*  
*Tabebuia* sp.  
*Epidendrum phoeniceum*  
*Zamia latifoliolata*

## MESA DEL LINDERO (600 feet)

*Ozandra lanceolata*  
*Jacquinia aculeata*  
*Ezoothea paniculata*  
*Hamelia lutea*  
*Leptocereus mazoni*  
*Acromomia crispa*  
*Roystonea regia*  
*Cordia globosa*  
*Trichachea insularis*  
*Dipholis salicifolia*  
*Tecoma stans*  
*Selenicereus urbanianus*

## MESA DE LA YAGRUMA (1,000 feet)

*Cecropia peltata*  
*Nectandra coriacea*  
*Ozandra laurifolia*  
*Clusia rosea*  
*Ficus aurea*  
*Cedrela mexicana*  
*Cordia gerascanthoides*  
*Celtis trinervia*  
*Passiflora multiflora*  
*Alchornea latifolia*  
*Victorinia regina*

## LOS LLANOS (1,500 feet)

*Dipholis juba*  
*Pithecellobium saman*  
*Cedrela mexicana*  
*Spondias mombin*  
*Ficus aurea*  
*Jatropha apetala*  
*Zanthoxylum martinicense*  
*Z. elephantiasis*  
*Didymopanax morototoni*  
*Cecropia peltata*  
*Roystonea regia*  
*Acromomia aculeata*  
*Psidium guajava*  
*Tournefortia hirsuta*  
*Ipomoea sidoides*  
*Solanum torvum*  
*Bignonia gnaphalantha*  
*Guarea trichilioides*  
*Cupania americana*  
*Alchornea latifolia*  
*Misanthea triandra*  
*Hufelandia pendula*  
*Ocotea leucozyylon*  
*Torrubia obtusata*  
*Eugenia jambos*  
*Citrus vulgaris*  
*Urera baccifera*  
*Bryum leoni*  
*Vitis caribaea*  
*Passiflora quadrangularis*  
*Sapium jamaicense*  
*Prunus occidentalis*  
*Sterculia apetala*  
*Cupania americana*  
*Guazuma tomentosa*

## VISTA ALEGRE (2,500 feet)

*Eugenia* sp.  
*Nectandra coriacea*  
*Cecropia peltata*  
*Miconia serrulata*  
*Clusia rosea*  
*Maregravia rectiflora*  
*Rhipsalis cassutha*  
*Hohenbergia pendulifera*  
*Aechmea nudicaulis*  
*Tillandsia excelsa*  
*Guzmania lingulata*  
*Alsophila* sp.  
*Cyathea arborea*  
*Hymenophyllum ciliatum*  
*Trichomanes* sp.  
*Polypodium duale*  
*Nephrolepis rivularis*  
*Asplenium* sp.  
*Adiantum* sp.  
*Oleandra articulata*  
*Odontosoria wrightii*  
*Calyptrotroma dulcis*  
*Euterpe globosa*  
*Bactris plumeriana*  
*Olfersia cervina*

Here, at Vista Alegre, the writer closes his account of the vegetation of Cuba. He knows no more delightful place to end a journey in tropical America than in an elfin forest where the vegetation seems

not to be of this earth, but of the world of make-believe, where Nature has combined all that is elfish with some of her most exquisite artistry (Fig. 64).



FIG. 64. The crown of a tree fern.

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## SOME FOOD COACTIONS OF THE NORTHERN PLAINS RED FOX

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Journal paper No. J-1131 of the Iowa Agricultural Experiment Station, Ames, Iowa. Project No. 598. The Fish and Wildlife Service (United States Department of the Interior), Iowa State College, Iowa State Conservation Commission, and the American Wildlife Institute cooperating.

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## SOME FOOD COACTIONS OF THE NORTHERN PLAINS RED FOX

### INTRODUCTION

The coactions between the northern plains red fox (*Vulpes regalis* Merriam) and its plant and animal associates were investigated on the Moingona Fox Range, from June, 1938, to July, 1941. The word coaction has been used by Clements & Shelford (1939, p. 103) ". . . to designate the enormous range of interactions among plants, plants and animals, and animals alone, since it involves not only the idea of acting together, but also that of urging or compelling." Research on the foods of red foxes has had a strong seasonal bias as the work usually was carried on only one or two seasons. This study sought to obtain data with greater depth through continuous observation over a period of three years. The meaning of food availability was broadly interpreted in this investigation because there is a tendency for predation to be proportional to the numbers of available prey (McAtee 1933). Furthermore, as popular belief held that red foxes possess remarkably efficient hunting prowess, it was important to attempt an evaluation of the extent to which they influenced the trends of prey animal populations.

Findings on red foxes in Iowa by Errington (1935, 1937) and many general notes contemporaneously gathered on other fox ranges have been used as background for the study.

My sincerest gratitude is due the United States Fish and Wildlife Service, the Iowa State College, the Iowa State Conservation Commission and the American Wildlife Institute by whose coöperative agreement the research was made possible. For counsel and encouragement I am deeply grateful to Dr. Ira N. Gabrielson, Dr. W. B. Bell, Mr. W. L. McAtee, Dr. H. H. T. Jackson and Mr. Leo K. Couch, all of the United States Fish and Wildlife Service; and to Dr. C. J. Drake, Dr. George O. Hendrickson and Dr. Paul L. Errington, all of the Department of Zoology and Entomology, Iowa State College, Ames, Iowa. The frank appreciation shown by Mr. Fred Schwob, Director of the Iowa State Conservation Commission, Mr. Taylor W. Huston and others of the Commission for the results obtained in the wildlife research program has served as a constant inspiration. The interest, contributions and friendships of those students who have been associated with the writer during the fox investigation are highly valued—Messrs. Lee Kuhn, Robert Moorman, Emmett Polderboer, Harry Harrison, Edwin Snead, Thomas Baskett and Ray Erickson.

For aid in identification of the more difficult food items I am indebted to Dr. A. C. Martin, Mr. Franklin E. May and others of the Section of Food Habits, United States Fish and Wildlife Service, to Dr.

H. H. Knight and Dr. Irving Fox of the Department of Zoology and Entomology, Iowa State College, and to Dr. R. H. Porter, Seed Laboratory, Iowa State College.

A debt of thanks is due Messrs. Andrew McLeod, Allen McLeod, W. R. Miller, Herman Rose, Joe Hull, Elmer Keeney and others on whose lands the work was carried out.

### THE MOINGONA FOX RANGE

The Moingona Fox Range is in the Des Moines River Valley about five miles south of Boone, Iowa. Intensive observations were made on an area of 2,010 acres, and an additional 4,000 acres of surrounding lands were examined at times.

The 2,010-acre area is bounded by the Des Moines River on the east and northeast. The river serves as a barrier, except when frozen in winter, and even then it is seldom crossed. Elsewhere the area is bounded by roads: the Boles Hill Road on the northwest, Hull Road on the west and southwest, and the River Road on the southeast. The River Road skirts the river through the area, and the east-west School Road also divides the range. The roads make all parts of the area accessible and aid materially in localizing "sign."

The rough terrain (Fig. 1) rises from about 860 feet above sea level at the Des Moines River on the east boundary to a little above 1,100 feet on the upland in the southwest corner. The major bottomlands lie close to the river and extend a short distance west along Bear Creek. West of the bottomland a network of short streams and drainage lines cut the slopes to an average of 30 to 35 percent.

Sandstone bedrock is exposed in several places, particularly along Bear Creek. Several large opened poackets of sand occur along Polly Creek. Nearly all the streams and drainage lines have sandy bottoms that record foot prints and other "sign" of animals during snowless seasons. The bottom of Polly Creek, with sand 6 to 50 feet in width for over a mile and dry throughout most of the year is ideal for "sign."

A wide range in annual temperature marks the region. In summer southwest winds accompany periods during which the temperature ranges above 100° F. The winter is severe with frequent northwest winds and usually one or more periods of some —20° F. temperature. The average annual growing period is 153 days (Reed 1940). The greater part of the average annual precipitation of 32 inches falls in spring and summer. The climograph (Fig. 2) demonstrates the general month to month weather progression and contrasts weather conditions during the three years of study.

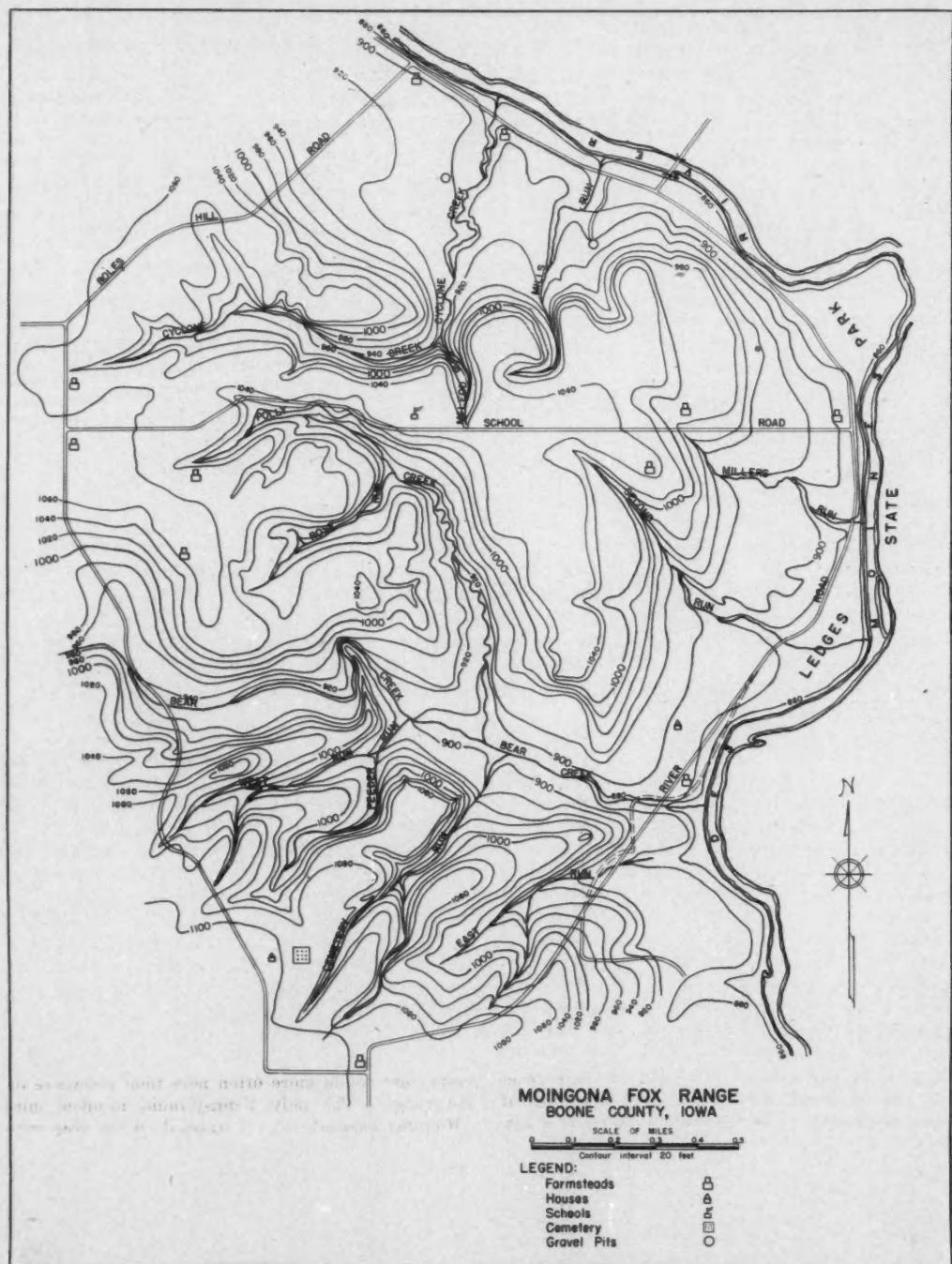


FIG. 1. Topography of the Moingona Fox Range.

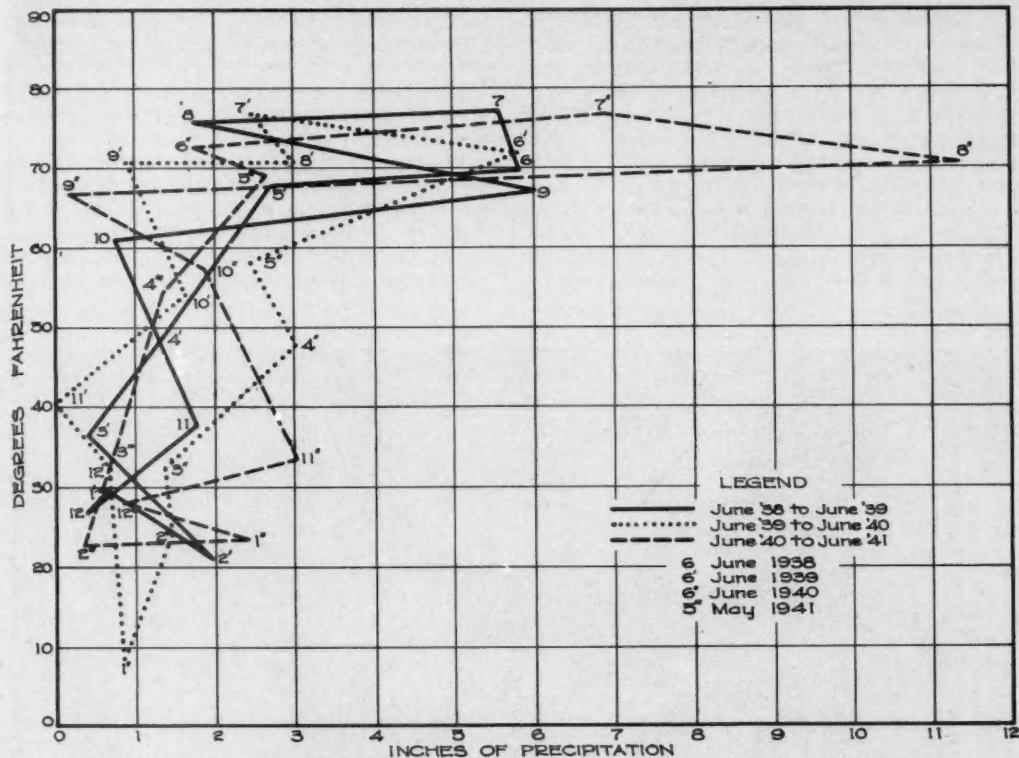


FIG. 2. Mean monthly temperatures and precipitation for each of the years studied.

The Range is in an agricultural community with 11 farmsteads, a rural school and a small cemetery. The topography requires that the fields be small, scattered and frequently irregular in outline (Fig. 3). As only the more level land is cultivated, the plantings detour gullies and rough places in the fields. On the 650 planted acres a corn-oats-alfalfa rotation of crops seems to be practiced generally. A percentage classification of the 1938-41 use of crop land was: corn 44, alfalfa 28, oats 15, soybeans 6, wheat 3, cane 1, and fallow 3. About 1,100 acres is in permanent pasture which lies largely on the steep, un-tilable slopes. Most of the available pasture area is grazed so closely, chiefly by cattle, as to leave no grassy cover suitable for mice. Each year some tree cutting in the pastures and field margins yields fence posts and fire wood, and permits greater growth of grasses for grazing. Severe erosion occurs in a few places.

Agricultural use of the land has greatly modified the natural state of biotic communities. Only fragments of natural vegetation remain. Least disturbed is that on the lowland adjacent to the river and within the boundaries of Ledges State Park. In this undeveloped part of the park, so far as is known, timber has never been cut. Here many large cottonwoods (*Populus deltoides*), American elms (*Ulmus*

*americana*), green ashes (*Fraxinus pennsylvanica*) and silver maples (*Acer saccharinum*) standing close together are hung heavily with riverside grapes (*Vitis vulpina*). Dense thickets of sandbar willow (*Salix interior*) cover the lowest and newest of this first bottom. Young box elders (*Acer negundo*) and occasional American elders (*Sambucus canadensis*) encroach on the field borders in the clearings.

None of the vertebrate animals seem to mark the bottomland environment proper. The zone of lowland adjacent to open water is characterized by the muskrat (*Ondatra zibethica*) and eastern green heron (*Butorides virescens virescens*), the latter absent in winter. The opossum (*Didelphis virginiana*), raccoon (*Procyon lotor hirtus*) and mink (*Mustela vison*) are found more often here than elsewhere on the range. The only Pennsylvania meadow mice (*Microtus pennsylvanicus*) trapped on the area were taken in bottomland clearings.

Except on a slope overlooking the river and within the boundaries of the Ledges State Park, the vegetation of the steep phase has been greatly disturbed. Remnants of the major plant units, oak-hickory (*Quercus-Carya*) community on southerly exposures and upland and maple-linden (*Acer-Tilia*) community on northerly exposures, are left with transition growths everywhere between. American aspen (*Pop-*

*ulus tremuloides*) in clumps, scattered red cedar (*Juniperus virginiana*) and service-berry (*Amelanchier canadensis*) remain. An interdispersal of typical southern plants and typical northern plants is indicated by a few large-toothed aspens (*Populus grandidentata*) and wild cherry (*Prunus pensylvanica*) from the north and the lance-leaved buckthorn (*Rhamnus lanceolata*) from the south. Hop-hornbeam (*Ostrya virginiana*) is the most numerous tree in some cut over tracts and blue beech (*Carpinus caroliniana*) occurs in several places. Western crab apple (*Malus ioensis*) and several species of red haw

(*Crataegus* spp.) are in clearings, particularly. Prickly ash (*Zanthoxylum americanum*), hazelnut (*Corylus americana*) and sumac (*Rhus*) are common. Typical spring flowering herbs are common except where bluegrass sod, together with typical weeds, is established.

An examination of the animals typifying the steep slopes reflects much of their nature. The southern woodchuck (*Marmota monax monax*), gray eastern chipmunk (*Tamias striatus griseus*), western fox squirrel (*Sciurus niger rufiventer*) and northern white-footed mouse (*Peromyscus leucopus noveborae*)



FIG. 3. Aerial photograph of the Moingona Fox Range. North at top.

*censis*) seem to characterize the mammal fauna. All of the dens used by red foxes for rearing their young were also in these slopes.

It is difficult to determine which of the birds mark the environment of the slopes. Although present to some extent over the entire area, the eastern cardinal (*Richmondena cardinalis cardinalis*), eastern goldfinch (*Spinus tristis tristis*), black-capped chickadee (*Penthestes atricapillus atricapillus*), white-breasted nuthatch (*Sitta carolinensis carolinensis*), northern blue jay (*Cyanocitta cristata cristata*), northern downy woodpecker (*Dryobates pubescens medianus*), hairy woodpecker (*Dryobates villosus villosus*), and red-bellied woodpecker (*Centurus carolinus*), are permanent residents on the slopes. Of nesting migrants the red-eyed towhee (*Pipilo erythrophthalmus*) seems to characterize the community of this steep phase best.

The relatively level crop lands, often weedy, are sometimes visited from the prairie by the common badger (*Taxidea taxus taxus*) and the white-tailed jack rabbit (*Lepus townsendii campanius*). The thirteen-striped ground squirrel (*Citellus tridecemlineatus tridecemlineatus*) is found in the undisturbed clearings. Baird white-footed mouse (*Peromyscus maniculatus bairdi*) and the prairie harvest mouse (*Reithrodontomys megalotis dychei*), are characteristic of the cultivated fields. Prairie meadow mouse (*Microtus ochrogaster*) and Goss lemming mouse (*Synaptomys cooperi gossii*) found in the cultivated lands, are most often trapped in the grassy fence rows around the fields. The cultivated openings have increased the attractiveness of the area for many species of birds, notably the eastern bob-white (*Colinus virginianus virginianus*). The few ring-necked pheasants (*Phasianus colchicus torquatus*) remain close to the open fields. Foxes do much hunting in and about the crop land clearings.

Some influential widely distributed vertebrates are not closely enough related to any part of the environment to characterize it. The white-tailed deer (*Odocoileus virginianus*) is re-established here by escape from a captive herd at Ledges State Park. The domestic dog (*Canis familiaris*) population varies widely in density and kind. Domestic cats (*Felis domestica*) are at farmsteads and an occasional feral cat is seen, particularly in fall and early in winter. Racoons, common on the bottomlands, by their "signs" are detected throughout the area. Although the focal points of mink activity are along Bear Creek and the Des Moines River, tracks of mink are often seen far up on the sandy drainage lines and occasionally on the upland. Striped skunks (*Mephitis mephitis*) usually remain close to their dens in the wooded slopes, but they often feed in the fields and sometimes dig shallow rearing dens there. Spotted skunks (*Spilogale interrupta*) are most common about the farm buildings. The long-tailed weasel (*Mustela frenata*) does not seem especially abundant.

The avifauna of the area as a whole is greatly

modified by migration, especially since the Des Moines River Valley seems to form a route of travel. Including migrants it is possible to list over 200 forms of birds from this locality of which only about 10 percent may be considered as resident. Forms that typify the region or are of influential importance are mentioned. The eastern red-tailed hawk (*Buteo borealis borealis*), Cooper's hawk (*Accipiter cooperi*), eastern sparrow hawk (*Falco sparverius sparverius*), eastern screech owl (*Otus asio naevius*), northern barred owl (*Strix varia varia*) and great horned owl (*Bubo virginianus virginianus*) are resident. The numbers of raptors are affected by control measures practiced at the nearby State Game Farm for the protection of propagated game birds. Horned owls, particularly, fall victims to the pole traps at the game farm. Eastern crows (*Corvus brachyrhynchos brachyrhynchos*) are always present, though not abundant. A small colony of turkey vultures (*Cathartes aura septentrionalis*) is resident in summer. A western bird, the American magpie (*Pica pica hudsonia*), is recorded for winter, 1939-40.

The animal community is not greatly affected by hunting, which is confined largely to cottontails and fox squirrels.

## FIELD TECHNIQUES

### "SIGNS" OF THE RED FOX

Greater returns are realized from concentrating on the scraps of evidence or "sign" left behind by a fox than from direct observations on the animal.

The track is the most frequent distinctive form of evidence. In general shape the track is oval with the longer axis taking the direction of travel. The toe pads are small, and the toes, particularly on the fore feet, may be spread on soft surfaces or when unusual weight is thrown on the fore feet as when reaching the bottom of a steep descent or when jumping. Structural differences between the fore and hind feet may be used to separate them. In comparison with the fore foot, the heel pad of the hind foot is about half as wide, and the two middle toes together with their claws appear to converge (Fig. 4). The hind foot is generally 5 percent smaller than the fore foot. The largest track measured on the area was that of a fore foot 2.8 inches long by 1.8 inches wide. Although tracks of adult males ordinarily are a little larger than those of adult females, tracks of an individual of either sex show variation in size on different tracking surfaces. Occasionally there is overlapping of size in adult males and females, and an additional variable is introduced by the presence of young animals. The mark of the heel pad in the track does not ordinarily project forward between the outermost toe prints on either fore or hind feet, though it may appear to do this where the foot sinks deep in soft mud or snow. The characteristic heel pad of the fore foot is bar-shaped, straight-edged to the rear. On such surfaces as mud and wet snow that are fine enough to hold



FIG. 4. Red fox tracks in mud. The upper impression is that of a hind foot while the lower one is of a fore foot.

the impression, the furry nature of the foot may be clearly observed.

Track patterns of the different gaits are similar to those of the domestic dog except that the tracks of the walking or trotting fox are usually in almost a straight line and not staggered (Fig. 5). In both walk and trot gaits the tracks may be from 9 to 16 inches apart. A fox may trot and take steps as short as those of a walk, but strides of 14 to 16 inches almost certainly indicate a trot. In the gallop the tracks appear in groups of four (Fig. 6). With each bound the two fore feet strike the ground in line while the hind feet are still in the air. Then the hind feet come to the earth, first the right and then the left, staggered and spread in advance of the tracks left by the fore feet. The length of each group of tracks and the distance between the groups increase with the rate of speed. Extreme distances between track groups in a gallop on level ground measure 30 to 88 inches. Undoubtedly size, age and condition of a fox affect spacing of tracks in the different gaits. Walking and trotting females, heavily pregnant, stagger their tracks noticeably.

One familiar with red fox scent often becomes aware of this odor before other "sign" is detected. Scent not only identifies the fox, but during periods when tracking conditions are poor, it may be employed to determine the presence and whereabouts of foxes. The method of urination, which appears to



FIG. 5. Track pattern of trotting red fox.



FIG. 6. Track pattern of a galloping red fox.

be after the fashion of domestic dogs, aids in determining sex. This is not always a reliable method of segregating sexes, for males occasionally urinate after the manner of females.

Fecal passages, or seats, may appear in form from a watery mass to a mucus-coated bone fragment. Typical seats of adult fox are shown in Figs. 7 and 8. In over-all length seats of adult foxes range from short fragments to 12 in., with an average length of 6.3 to 7.4 in. Generally there are two to four segments to a passage and as many as nine were observed. For 100 seats from caged wild red foxes measured at their largest diameter the average was 0.5 in., the smallest was 0.32 in., and the largest was 0.64 in. Within these size limits the fecal passages of the captive animals noticeably varied in size directly with the amount of food eaten. The largest red fox seat found, apart from a few that appeared to have expanded after defecation because of excessive ground moisture or other cause, was 0.75 in. in diameter. Seats containing the remains of fruits or insects are usually large in diameter.

A coat of mucus marks the red fox seat and frequently aids in identification. Unless previously removed by weather or insects the dry mucus may often be rubbed off in a fine powder. In outward color the seat grades from black or dark brown to light gray. Often a shade of green, discernible

somewhere on the seat along with the basic color, seems to be somewhat characteristic of red fox feces. The passages have an odor distinctive of the fox. At first it is possible to detect the odor at the outside of the seat, but as the outside dries it is necessary to break the material. In occasional seats the odor is detectable in some of the segments and not in others. The fox odor may be suppressed by that of remains of food such as fruit in fresh feces.

"Sign" is often present where the red fox beds down to rest and to dress its coat. The circular bedding spot is usually about 15 inches in diameter; its form may best be seen in snow (Fig. 9). In a snow bed loose hairs are easily seen. There are times in winter, particularly when a trail is old and snow has melted to enlarge the original tracks, that the evidence about a bed may be used to reassure a tracker that the trail is that of a red fox. In dressing the coat a fox uses its teeth as a card and loose hair accumulated in the mouth is tossed aside in small bunches. Most of the bunches are marked by two holes one-eighth inch in diameter (Fig. 10), presumably from canine teeth. Hair also clings to burs and other hooked fruits that are plucked out of the coat. "Signs" of coat dressing are especially noticeable in spring when the animals are shedding.

In feeding a red fox may leave scratch marks that are conclusive or give support to other evidence.

Teeth marks sometimes show in the flesh or skin of prey. The distance between the punctures of the right and left canines of either jaw may sometimes be measured to aid in identifying a predator. The linear measurement between the tips of each pair of canines was taken on 20 red fox skulls selected at random from animals killed in December and January in Iowa. The mean distance between the tips of the maxillary canines was 0.83 in., the greatest 0.92 in., and the least 0.72 in.; the mean distance between the tips of the mandibular canines was 0.74 in., the greatest 0.84 in., and the least 0.68 in. The marks of the canine teeth are seen principally in the pectoral region of larger prey.

Experiments with caged adult red foxes indicate that about one pound of food is eaten at a feeding. Mice are ordinarily bolted entire, whereas unless more than one fox is feeding part of a cottontail is left. When birds are eaten, feathers are often neatly sheared off close to the base (Fig. 11). The part of the feather that is cut off remains at the feeding site to help identify the feeder as a fox, while the bases of the feathers left in the flesh appear in the seats. Something of the strength of the jaws of an adult fox is seen in the ease with which the bones of cottontails, domestic chickens (*Gallus gallus*), and ring-necked pheasants are crushed. That a young fox does not possess that same strength, may be seen in its feeding. While living in dens the young commonly leave a cleanly licked pelvic girdle, hind legs and a section of the vertebral column after feeding on a cottontail.

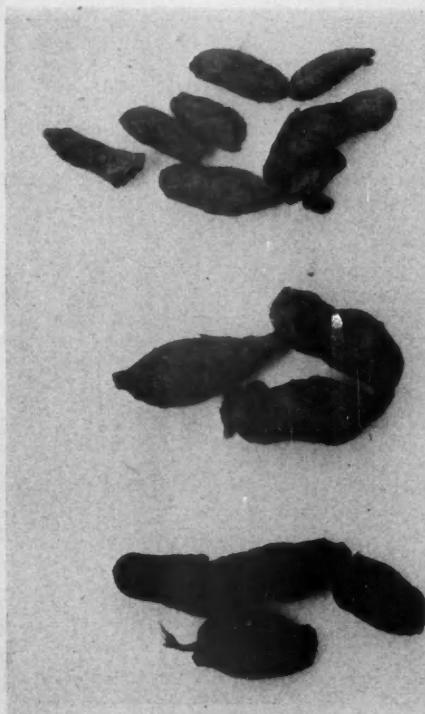


FIG. 7. Fecal passages of adult red fox. About one-half natural dimensions.

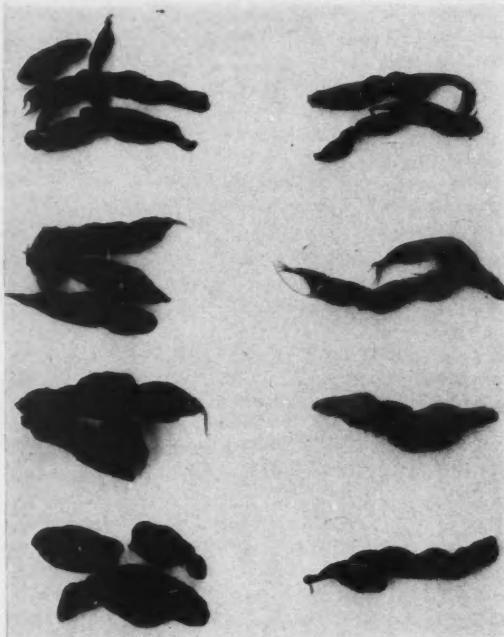


FIG. 8. Fecal passages of adult red fox. About one-third natural dimensions. The somewhat larger passages on the left were from the Big Wall Lake Area where food was abundant while the smaller passages on the right were from the Moingona Fox Range where food seemed barely available. The passages were taken at random from collections made in February and March, 1941.



FIG. 9. The bedding place of a red fox.

Although there seems to be no set order in which parts of prey are eaten, it is obvious that more often than not the head and neck of domestic chickens, ring-necked pheasants, and cottontails are among the parts first taken and that the hind quarters are among the last parts to be eaten. The abdominal viscera, feet and tail of cottontails are frequently left uneaten. That part of the wings largely beyond the humerus of large birds such as pheasants and domestic chickens (Fig. 12) is not usually eaten. Eggs, such as those of the pheasant, that have been fed on appear to have had about one-third of the shell bitten out, apparently most often from the side. A coarse, broken edge is seen on the remaining part, and it is usually licked clean of the last trace of contents.

Additional "signs" aid in collecting life history data. Clotted blood in the urine along the trail of the female may be evidence of the close of proestrus. Double and parallel trails may indicate a tendency to pair, and evidence of breeding may be seen on the trails. After breeding activity is underway the animals begin to scratch the accumulated debris and soil out of dens which were only visited or rarely used as refuge previously. Several dens on the range are cleaned out, but most of the activity is generally centered about the den in which the young are to be born. Often food is brought to the chosen den prior to birth of young. There is gen-



FIG. 10. Examples of loose fur tossed aside by the red fox dressing its coat. About two-thirds natural dimensions.



FIG. 11. Feathers sheared from the carcass of a ring-necked pheasant by the red fox.



FIG. 12. Remains of ring-necked pheasant left by red foxes.

erally enough "sign" at a rearing den to identify the occupants.

On this range the vegetation was so open that foxes did not need to open trails. General travel routes taken by foxes along such landmarks as ridges and drainage lines were recognizable. Of a less permanent nature were such routes of travel as stock trails, dead furrows and field roads. As a rule a fox usually did not follow the land mark far, but instead seemed to come upon the land mark, pass along it for a short distance and then work away from it. In the aggregate there seemed to be considerable traffic along strategically located routes.

An outline map traced from an aerial photograph was used in the field (Fig. 13). Each section was divided into 6.4-acre squares, which were numbered from left to right, beginning in the northwest corner. The squares were used as a more accurate means of locating observations. For example, a seat found on

a stock trail may be given an abbreviated locality record as follows: 20-73, which means that it was in division 73 of section 20. Usually an additional note was added such as: "stock trail, 2 paces N of NE corner of fallow field."

#### STATUS OF POTENTIAL FOODS

Phenological data, lists of kinds, figures on the amounts and notes on the availability of potential fox foods were extremely important. In addition to knowing something of the kinds of natural foods available to the foxes, a knowledge of the kinds of domesticated plants and animals found on the local farms was helpful.

Records were maintained on the availability of seasonal foods such as fruits, insects, and the young prey vertebrates. Domestic and wild animal casualties of the roadways, hunting seasons, diseases, harvest operations, burning, flooding, drought and severe winter weather often affected the availability of foods.

In addition to general notation of the relative amounts of food present from year to year, specific inventories of prey populations were conducted. In order to obtain quickly some figures on the relative numbers of small mammals, 100 traps were operated at 1-yard intervals for one night in each of three selected parts of the range in October, 1938. In 1939 a more systematic inventory of small mammals was undertaken. One hundred traps for capturing small mammals alive were operated in lines of 10 in a purposive sampling of plots along a transect, 0.2 mile wide by 1.0 mile long, through the center of the range from south to north (Fig. 13). Each line of 10 traps was set on the north-south axis through the exact center of the 6.4-acre quadrats staggered regularly along the transect. At first the traps were placed at one-rod intervals; later the interval was increased to a chain. Throughout the period, from March 1 to October 6, 1939, and from June 1 to September 19, 1940, commencing on or as near as possible to the first day of each month the traps were operated until animals not previously taken ceased to appear with regularity. In 1939 conventional methods of marking the trapped animals were used, but in 1940 Monel metal fingerling tags were fastened deep in the ear. It was thought that such marking might yield added information if the tagged animal was found dead or was eaten by a fox and the tag, resistant to digestion, was recovered in analysis of the feces. The attempt was made to calculate the populations of small mammals to the acre according to the method suggested by Dice (1938). The method is based on the assumption that a line of thoroughly efficient traps may be expected to denude an area extending for one-half the mean width of a cruising range beyond each end of the line. Sufficient figures to permit this calculation were obtained only for the northern white-footed mouse. The mean width of the cruising range of this species was adapted from the studies

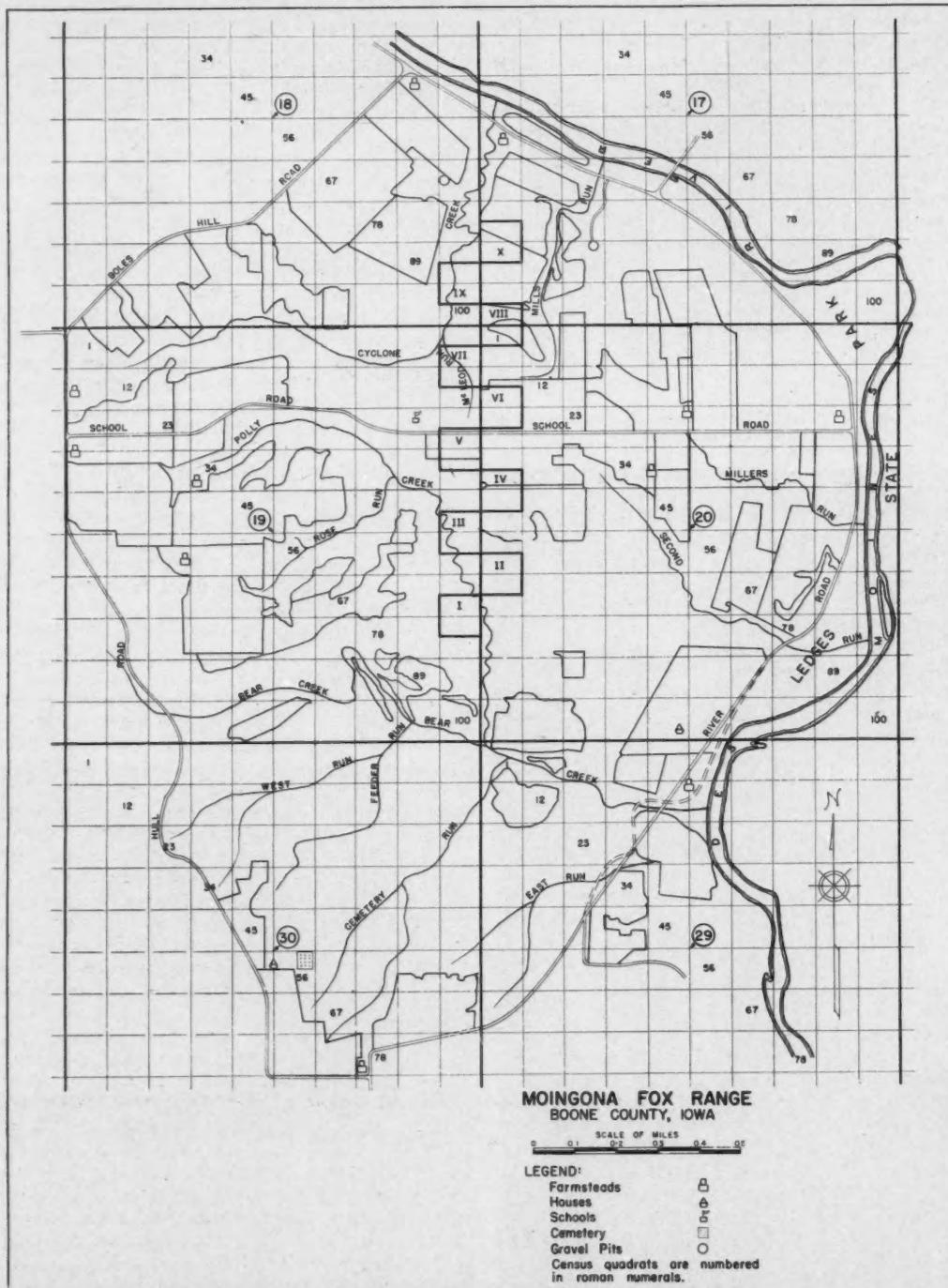


FIG. 13. Outline map showing grid system used in recording field evidence. Quadrats used in the estimations of prey populations are also used.

of Burt (1940) and from contemporary work on the Moingona area. In computing the population no attempt was made to differentiate between cruising ranges of the different age groups or sexes. It was thought fitting in this investigation to use a mean width of cruising range that would be reasonably representative of both sexes and the several age groups. The mean width of the cruising range used for the northern white-footed mouse was 250 feet. For other species of small mammals the data did not support more than statements of relative abundance.

Cottontail populations were estimated in summer by the pellet count method (Hendrickson 1939) and at other times by a flush count using a one-rod flushing front. The counts were made periodically on the same 10 6.4-acre quadrats used in the small mammal inventory. As a check on the data obtained, from the systematic counting on the quadrats, additional counts were made at other places on the area.

Covey track counts of bob-whites were made each winter over the entire range according to the technique described by Errington & Hamerstrom (1936). Throughout the late summer and early fall all quail families encountered were noted and where possible, counts of the number of individuals in each family were made.

As there were not many ring-necked pheasants, the concentrations of birds in winter were widely separated and a fair flushing count could be made at that time. Other estimates were based on an accumulation of direct observations made while working over the area for fox "sign" and making counts of other prey animals. Roadside counts of pheasants were made on the nearby prairie sections of Boone County, and this information was available for checking the population trend.

#### GENERAL ROUTINE IN THE FIELD

The field routine underlying this investigation was centered primarily about the necessity of keeping constantly in touch with the activity of the resident foxes and of collecting fox scats with regularity. Field work was greatly simplified whenever a good tracking snow was on the ground, excepting that it was sometimes more difficult for the observer to get about. (See Fig. 14 for snow depths.) At such times, in order to check on the current movements of the foxes after a new snow, all of the roads around and through the area were observed for fox tracks from a slow-moving car and by walking. The leads found in this manner were then used as guides to where the most productive tracking might be accomplished. The trails in the snow were not always easy to follow when the snow was deep and loose, encrusted, thawing or drifting. "Sign" found along trails in a good tracking snow was usually excellent and furthermore could be dated as having been made by the fox sometime during the time interval since the last snow, the last thaw, or the last visit of the observer. During snowless times field work was less productive. The entire area was then cruised period-

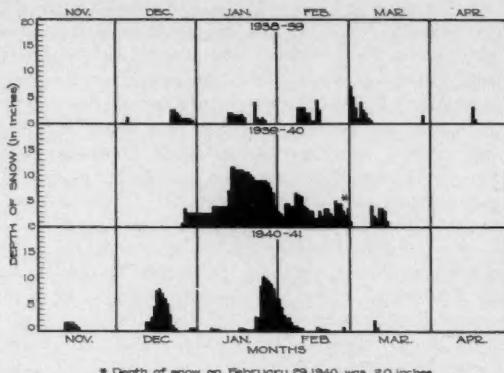


FIG. 14. Average depths of snow on the Moingona Fox Range during the three winters studied.

ically in order to maintain a perspective of the activity of the resident foxes. On such cruises a route was followed through all the places most likely to yield "sign" of foxes and yet touch in all parts of the range. The same procedure was followed when the focal point of fox activity was lost as when a family of young foxes moved to a new den. At other times observations were concentrated in the current theater of major activity. Regular visits were made over the routes through the current theaters of activity, weather and other duties permitting.

Efforts were made to minimize undesirable contact with the foxes. No attempt was made to observe the foxes directly except at rearing dens, and then it was done largely to determine the number of young. Den sites were usually avoided until it was known that the family had moved to a new location. On the few occasions when a fox trail was followed forward, the information obtained was not of the nature desired, and the time involved did not seem justified. The fox either detected the observer and thereafter was busy reacting mainly in relation to the tracker, or it was discovered bedded down. A fox found bedded down usually remained at rest until started and then it escaped from view as rapidly as possible.

Along the snow-free routes bare surfaces were checked for tracks. When the ground was softened by rain or thaws tracks were registered on nearly any bare surface. Likely places were ditch and gully bottoms, sand bars, low terraces subject to flooding, roads, stock trails and stream margins. During dry periods negative evidence was unreliable because tracks registered only in isolated places along stream margins, around seepages and dusty roads or stock trails. Dusty stock trails and roads were not very good because the tracks there were soon concealed under the dust from passing traffic. Cultivation of land also provided tracking opportunities, particularly the "dead" furrows in plowed ground. Soil disturbances such as those produced by the

Shaw pocket gopher (*Geomys bursarius*) seemed attractive to foxes. Sometimes after rains the foxes climbed on the boulders with muddy feet and left recognizable prints. This tracking evidence was especially valuable in densely vegetated areas where there were few areas in which to read "sign." Sometimes it was important to distinguish tracks seen on one visit from those seen on another visit. This was done by scratching a circle in the soil around some of the old tracks and inscribing the date of the visit within the circle. Another method was to scratch a symbol on each trail along a stretch of the route and record the symbol used in the field notes for that day.

On snow trails two and even more foxes were known to have passed over the same trail, each stepping carefully in the tracks of the first. When the trail was followed, places, such as on steep slopes, appeared where the tracks separated. Such splitting of tracks aided in estimating the number of foxes on the area. Such estimations were made with care, for a fox was known to have circled and retraced its trail. As foxes also followed in the tracks of other animals, close scrutiny was necessary.

When theaters of activity were located by tracks and other "sign," it was finally necessary to locate and interpret evidence of fox feeding. Often there was no evidence that fox had fed on an animal, much less killed it, and food caches beneath loose materials were easily overlooked. On noting small feathers of birds and tails of cottontails in the open it was frequently worth while to work into the prevailing winds to locate the remains on which foxes had fed. Small feathers were sometimes found where they had settled into the tracks of a fox trail in deep snow. At first it appeared that the feathers had fallen from a bird carried by the fox. Later it was found by working from such feathers into the wind that they were often the castoff remains of the meal of a hawk or an owl.

Fox seats, collected in a variety of locations, were usually in places where the vegetation was low, scant or absent. Seldom was a particular location used for defecating with any high degree of frequency. Boulders were used as places for defecation, particularly when there was considerable water on the ground as in spring or after a hard rain. Such locations furnished no more than about four or five seats during a year's observation. It seemed that during wet periods the number of seats found on quick-drying surfaces such as stones, logs and low stumps increased. Sometimes a stretch of dry, sandy drainage line or a bare ridge yielded 2 to 10 seats a week for as many as 6 weeks, and then none or very few for several years. Such locations, usually located in late summer, probably indicated a foal point of family activity after the dens had been abandoned. An exceptional place of defecation was a dog carcass, to be discussed later.

The collection of fecal passages in snow was largely a matter of getting on trails and following them until

a seat was found. In open fields where there were a great many trails it seemed conservative of time to cast over the field at intervals which permitted observation of all the ground. Seats and other "sign" were in this manner located without laboriously tracing out each of the trails. When there were no snow trails to follow, the observation routes along stock trails, drainage lines, ridges, streams and roads and certain places on and near these routes merited attention in the search for seats. Sandy washes, silt beds and gravel outcrops were examined for seats. Many seats were found along the stock trails, field roads and drainage lines without apparent relationships to anything but the route itself.

On snow trails it usually was relatively easy to determine the period of time within which defecation occurred. On other occasions, the time of defecation was estimated from the date of the last observations in the locality together with other "sign" present. On the routine trips over the area all the likely places of defecation were carefully and methodically inspected. A seat found on a subsequent trip was usually dated as between visits. Because seats were missed even with the most exacting observation, other evidence of time of defecation was examined. In the examination the seat was usually tested for odor as it was determined with caged foxes that the characteristic odor associated with the seat was generally difficult to detect after several days' exposure to the weather. Following a light rain the pits left by the rain drops were visible on the soil around the seat but not under it, or small particles of soil might have been pitched up on the seat by the pelting drops. Severe rainstorms broke up and washed away seats, particularly those composed of insect or fruit remains or previously pulled apart by arthropod scavengers. The age appearance of tracks around the seat was helpful. In extremely fresh seats the mucus was still intact and the seat was soft and moist. The effect of weather on the seat mucus was employed to some extent in determining the probable period of defecation. In summer, observations on the arthropods attacking the seat seemed of assistance in estimating the time of defecation, for these scavengers did not appear to feed on old seats. Knowledge of the time of the last cultivation of fields often provided a definite time bracket for dating seats found in cultivated fields. This problem of dating seats for the period of time in which defecation probably occurred was largely a matter of applying common sense reasoning to each situation.

A seat as collected was placed in a paper bag on which the date, probable time of defecation and locality were written. At the laboratory, the food remains were identified and recorded. Methods used in fecal analysis will be discussed under the section on food habits.

Another field technique that appeared worthy of attention is that of marking remains of prey found in the field. Monel metal fingerling tags as employed in censusing the small mammals were also used to

mark food remains in order that they might be identified on subsequent visits. Also, fingerling tags were folded and shoved into the flesh of prey with the hope of retrieving the tags from feces.

In good tracking snows attempts were made to obtain quantitative measurements of the fox's relationship to different cover types by recording the number of paces taken along trails in each type. The method did not prove very productive because more often than not the trail of an individual could not be followed far enough to permit sufficient measurements.

#### HOME RANGE, MOVEMENT AND LIFE HISTORY

Following an extensive review of literature relating to the theory of territory Nice (1941, p. 467) concluded that "Although a great many mammals have 'home ranges' in general these do not seem to be defended with the vigor shown by many birds and fishes." If proof of territorialism requires that emphasis be placed chiefly on defense of the individual or the social group, then the data here to be reported do not strongly support territorial behavior. If, on the other hand, positive reaction to a particular place and familiarity with the environment are manifestations of territory then territorialism is characteristic of the red fox.

Sportsmen who follow hounds know that red foxes tend to occupy particular areas, often locally known as ranges. Seton (1929) recalled that well-known foxes were reported as usually found within three or four miles of their presumed headquarters, and suggested that an individual red fox lived in an area of not more than five miles in diameter and did not ordinarily range that far. From January to August, 1934, a red fox (*Vulpes fulva*) family was studied on the Edwin S. George Reserve near Pinekney, Michigan, by Murie (1936), who reported that the foxes probably performed most of their hunting within the 1,200 acres of the reserve, but that their tracks were seen along the fence where they had passed in and out; and he thought that the area used for intensive hunting would probably have been considerably larger if the hunting had not been so much better within the reserve than on the surrounding farms. Hamilton (1939, p. 304) held that "A red fox, when started by hounds, will circle in its own square mile of territory unless pressed, when the harassed beast will enter unfamiliar terrain. When the hounds are shaken, the fox soon returns to its own homesite." The observations made on the Moingona Fox Range indicated that an arc drawn on a one-mile radius would ordinarily circumscribe the movements of the resident individual, pair or family.

Life history events and the closely related intra-specific social relations may be expected to influence the response to the fundamental need of food. The general activity of the red fox, naturally centering on the family as a social unit, annually progresses

through a winter breeding and pre-denning period, a spring and early summer denning period, a late summer and early fall period in which the young live free of the den and family ties gradually relax, and a period of dispersal.

The red fox is monoestrous (Enders 1938). In this region oestrus in the red fox usually occurs sometime during late December and early in January. On the Moingona area there was a gradual tendency for tracks, seats, beds and other "sign" to increase in intensity in certain places at the onset of the breeding season. Double and parallel trails of foxes traveling together were frequently seen. Blood, possibly marking the close of pro-oestrus, was found in the urine of a female fox on but two occasions, once on December 23, 1938, and again on January 24, 1941. At this time the males particularly seemed to increase their propensity to leave urine "scent." One male left its "scent" 12 times within a quarter of a mile after leaving its bed. Dens, often well concealed with snow, were visited and marked with "scent." The apparent directness with which these dens were located seemed to show a familiarity with the area that indicated an association with the range of considerable duration.

Serving to emphasize the sometimes dimly visible concentrations of "sign" of local foxes near the center of their ranges was the occasional trail of a transient fox. An excellent example of this was observed in good tracking snow on January 18, 1938. The trail was picked up about 100 yards southwest of the bridge across the Des Moines River. It was followed northwest across the river for about a mile beyond and when left it was seen proceeding in the same general direction up the river. Then the trail back-tracked southward through the area and for about a mile and a half beyond River Road where it was left still leading southward. Among fox hunters such an animal is often known as a "traveler," and the experienced hunter seldom attempts to stalk its trail.

Although there was again a confusing array of trails throughout the area in the winter of 1939-40, by January 4 the observer noted a tendency for the "sign" to concentrate in two theaters, one north of School Road and the other south. Perhaps a manifestation of territorialism relating to this division of activity was an incident that occurred on January 10. While Charles Yocom and the writer were standing on School Road in the northwest corner of Section 20 between the two theaters of intense activity, a large red fox called attention to itself by yapping at the observer for several minutes from a position about 100 feet south of the road in a field of corn stubble. The animal, decidedly defiant in its manner, finally retreated out of sight in a southeast direction. Inspection of the tracks showed that the fox had approached from the southwest directly toward the position of the observers. Direct observation or "sign" readings indicating intra-specific strife were not made. This is the kind of behavior, however,

which in animals such as foxes might easily escape attention.

The foxes became increasingly conservative in the extent of their movements as the time for birth of the young approached. About the time the pups were born the scope of activity of the adults was within a one-half mile radius of the natal den. On February 28, 1939, an 8-inch snow ceased falling at 1:00 p.m. Careful inspection of the area showed that by noon of March 2, no fox trails were beyond one-fourth mile from the den. By March 4 much of the snow had melted. A new 3-inch snowfall ceased at 6:00 p.m., March 5, and on March 6 snow trails were found as much as one-half mile from the den. Several observations of pairs of foxes moving together or bedded down not far distant from each other were also made during the pre-denning period. Dens may have been visited and "scented" during the winter, but it was not until late in February that foxes began to prepare dens for use by cleaning them out and enlarging them (Fig. 15). Because many dens

defecated early that morning was found on a rotted-down stump about one-half mile directly south of the place where the tag had been left. This may serve as fair evidence that a fox familiar with the area was still resident at that time.

Perhaps in part indicative of territorial behavior is a series of incidents that began in the pre-denning period and extended into the denning period of the foxes in 1939. A local aged farm dog was shot in mid-February at a point on the area about 200 yards southwest of the den in which the fox cubs were subsequently born (Fig. 16). When the dog carcass was inspected on February 18 there was no "sign" of foxes about it. By March 1 especially heavy "sign" was noted about the nearby den, indicating that this was probably the den in which cubs would be born. On March 6 a strong odor of fox "scent" attracted attention to the nearby dog carcass which had been anointed liberally with fox urine and decorated with a number of seats. On March 14 the dog carcass was again visited and eight seats, defecated since the last visit, were collected. The carcass was still being heavily "scented." A hind leg and the tail had been pulled free of the frozen body. The tail was nearby, but the leg had been dragged 200 yards to the north. By March 21 the foxes seemed to have lost interest in the dog when only one seat was collected. It could not be determined in the field that the foxes had ever eaten any of the animal, and analysis of the seats did not reveal the remains of domestic dog. Early in spring, 1941, two farm dogs were shot and left in the south part of the area. Although their carcasses were carefully inspected on every visit to the area no evidence was ever found that they had been approached by foxes though trails frequently passed nearby. As indicated earlier no fox pups were raised on the range that year, and this may have had something to do with the absence of interest in the dead dogs.



FIG. 15. A den opened up by a red fox.

were conditioned in this way, the den in which pups were to be born was usually difficult to determine. In 1941 as in 1939 and 1940 all the usual advance preparations for raising a family took place: dens were cleaned out, and food was even deposited in an entrance of one. Cubs were never seen in 1941. Probably a pregnant female fox shot near the cemetery late in February was out of the pair that had been resident on the range. Fox "sign" continued to appear in the southwest part of the area in considerable amount until late in April. Thereafter throughout the summer only an occasional track was found, generally in the southeastern part of the area. On March 29 a 1-inch cube of beef heart marked with a numbered Monel metal tag was left at a place where a fox had apparently fed on a cottontail in Polly Creek just opposite the den in which the young were born in 1939. Two days later, March 31, a fox seat containing the tag and that had probably been

The experience of the silver fox fur industry indicates that the native red fox probably has a gestation period of about 51 days. The field evidence roughly supports a similar time between the breeding season and the birth of the young. In 1939 fox pups were born in a den in the side of a deeply incised gully just off Polly Creek sometime late in March. The fox pups remained in the den of their birth until they were four or five weeks old when sometime during the period between April 22 and 28 they moved into a new den about one-fourth mile southeast. All of the occupied dens and the sequence of their use in 1939 are shown in Fig. 16. Although it frequently meant failure to obtain seats and records of food items at the den the precaution of not approaching the den until it was relatively certain the occupants had departed usually was followed. The pups were seen for the first time at this second den; there appeared to be three in the litter. On May 6 or 7 the pups moved back into the natal den. This time two nearby dens were brought into use as outlying retreats. The pups were seen here twice before they

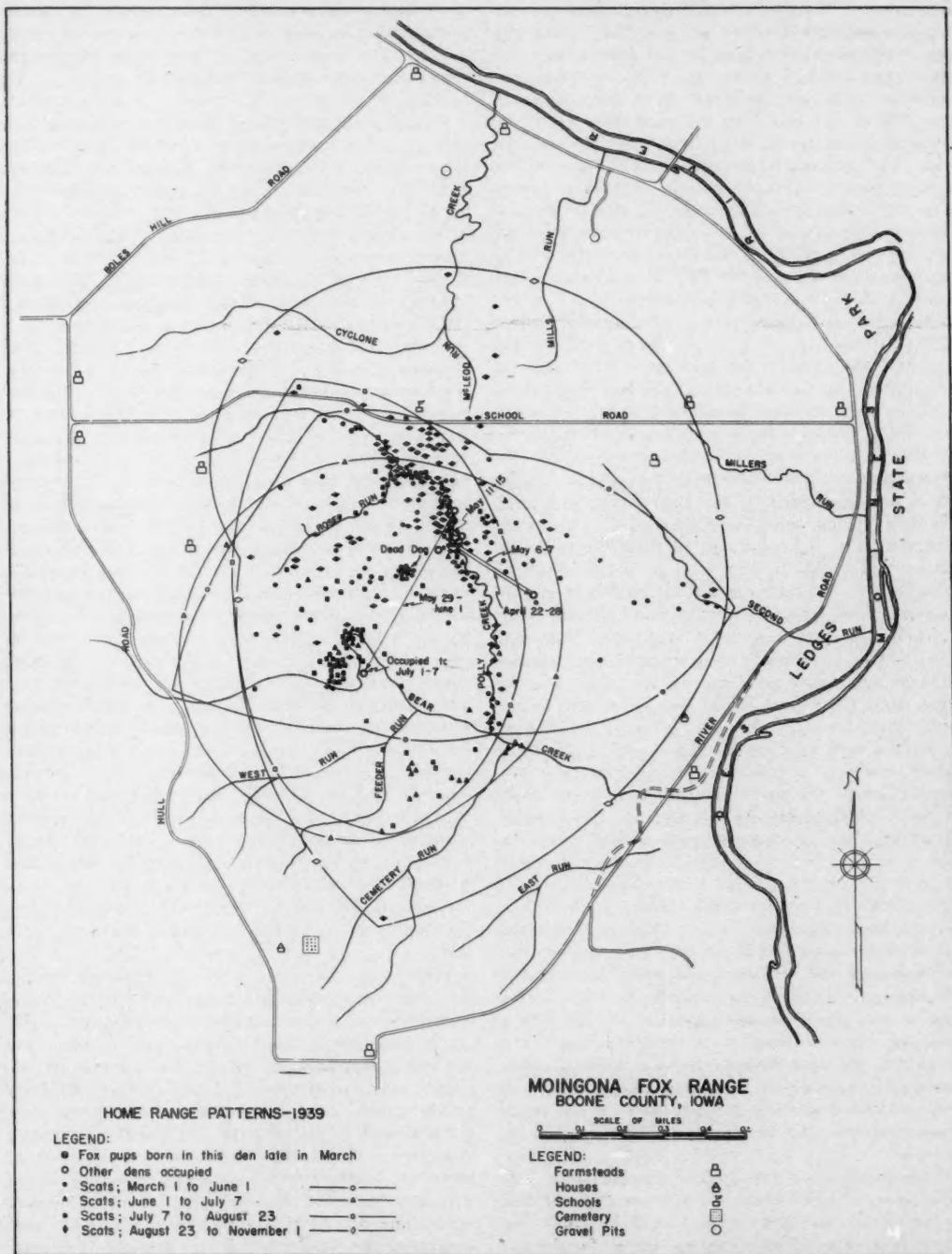


FIG. 16. Den sites, direction and time of movement between dens, seat locations and interpolated home ranges, 1939.

went north about one-tenth mile to another den sometime between May 11 and 15; again three was the largest number in view at any one time. This den was evacuated between May 29 and June 1 when the pups were near 10 weeks old. The new den was about one-half mile southwest in a steep slope on Bear Creek. At this time the pups were known to have traveled as far as one-fourth mile from the den. Sites of all fox seat collections on the area exclusive of those picked up at the rearing dens were spotted on a map (Fig. 16); then together with tracks and all other "sign" located, an outline interpolation of the range occupied by the family from March 1 until the time of the move to the Bear Creek location was drawn. This interpolation of range, as all others made in this study, quite probably does not include all the extremes to which the adults may have gone, for when one considers the scarcity of fox "sign" on the periphery of the home range the ease with which it might be passed over is evident. It is reasonable, however, to consider the outlined area as all that is ecologically significant, especially as related to this investigation of food coactions.

The pups remained in the Bear Creek den until sometime during the period June 1-7, when they appeared to have finally severed their ties with the den as home. The young were probably about 14 weeks old at that time. An interpolation of the range occupied while the family was headquartered in the Bear Creek den is shown on the map (Fig. 16).

In 1940, as has already been reported, two families of foxes established residence on the area. The female on the north part of the area gave birth to her young in a den on Cyclone Creek (Fig. 17) about the second week of March. The young of the other family were born in a den on Second Run (Fig. 17) in mid-March. On April 8 it was possible to count six pups playing outside the Cyclone Creek natal den at one time. Between April 9 and 11, when the pups were four or five weeks old the family moved east about one-third mile to a new den in the steep south bank of Cyclone Creek near the mouth of McLeod Run. Six pups in the litter were counted several times during their stay in this den, particularly because the den site could easily be observed.

A dead cottontail, located on the butt of a haystack in 19-3 April 16, was tagged in the ear with a metal tag. It was found about two-thirds mile away at the den site near McLeod Run on April 21, thus indicating something of the size of the range of an adult at that time. An interpolation of the range occupied during the period April 1-22 appears in Fig. 17.

When the pups of the Cyclone Creek family were about seven or eight weeks old between April 28 and 30 the family moved to a den on Mills Run. As indicated in Fig. 17 the Cyclone Creek family appeared to bring into simultaneous use several dens during the ensuing period May 21 to 31. So far as known the young foxes soon after loosened their ties with the den as home at 12 or 13 weeks of age. In

order to make the time span for the range interpolations agree and to cause the mapping to be less formidable, the interpolation for the period April 23 to June 20 extends almost three weeks beyond the time when the Cyclone Creek family ceased to live in the dens.

The pups of the Second Run family remained in the natal den until between April 20 and 22. The largest number of pups seen here at one time was five. An interpolation of the range occupied from April 1 to 22 is outlined in Fig. 17. When the pups of this family were near five weeks of age the family moved three-fourths mile southwest to a den in the north slope of the ridge between the junction of Bear Creek and Feeder Run. Between April 26 and 29 the family moved northwest one-tenth mile to a den that had been occupied by the foxes in 1939. Between May 1 and 3 they evacuated to a den one-third mile southeast on Cemetery Run. The five pups in the litter were counted again here on May 8. This den was occupied until between May 9 and 12 when the young moved one-sixth mile southwest to a new den. On May 22 some of the pups were again seen at the den on Cemetery Run. A young male of the litter was found dead within 200 feet of this den May 31. The animal weighed 6.4 pounds at an estimated age of 11 weeks. The thorax was punctured as by a single bullet, and the hind legs, particularly the right one, were severely hamstrung. The tooth marks in the skin were such as might have been delivered by litter mates. The family immediately moved directly north two-thirds mile to the 1939 natal den. During the period June 8 to 10 the family again moved south, this time one-half mile to a new location on a low bank on the north side of Bear Creek. They remained at this new den until between June 26 and 30, after which they seemed to relax their ties with the den as home. The pups were thought then to have been about 15 weeks old. An interpolation of the territory occupied by this family from April 23 to June 20 appears in Fig. 17.

Even after the pups terminated life in the dens the family ties seemed to continue unbroken into the fall.

Where dens formerly were the hubs of activity now there were rallying stations. These are clearly marked by the concentrations of seat locality marks on the home range maps (Figs. 16, 17). All of the stations were characterized by the absence of tall, dense cover. Stretches of dry sandy stream beds, closely grazed pastures and the more or less bare earth of well-cultivated cornfields seemed particularly attractive. Cornfields, while allowing freedom of movement, still provided excellent concealing cover.

In 1938 intensive observations were not undertaken until June 6. At that time the young foxes were occupying the den in which the pups of 1939 were born, and the same nearby dens were being used as outlying retreats. A squeaking noise produced by pursing the lips against the back of the hand was employed to coax two pups to the entrance of the

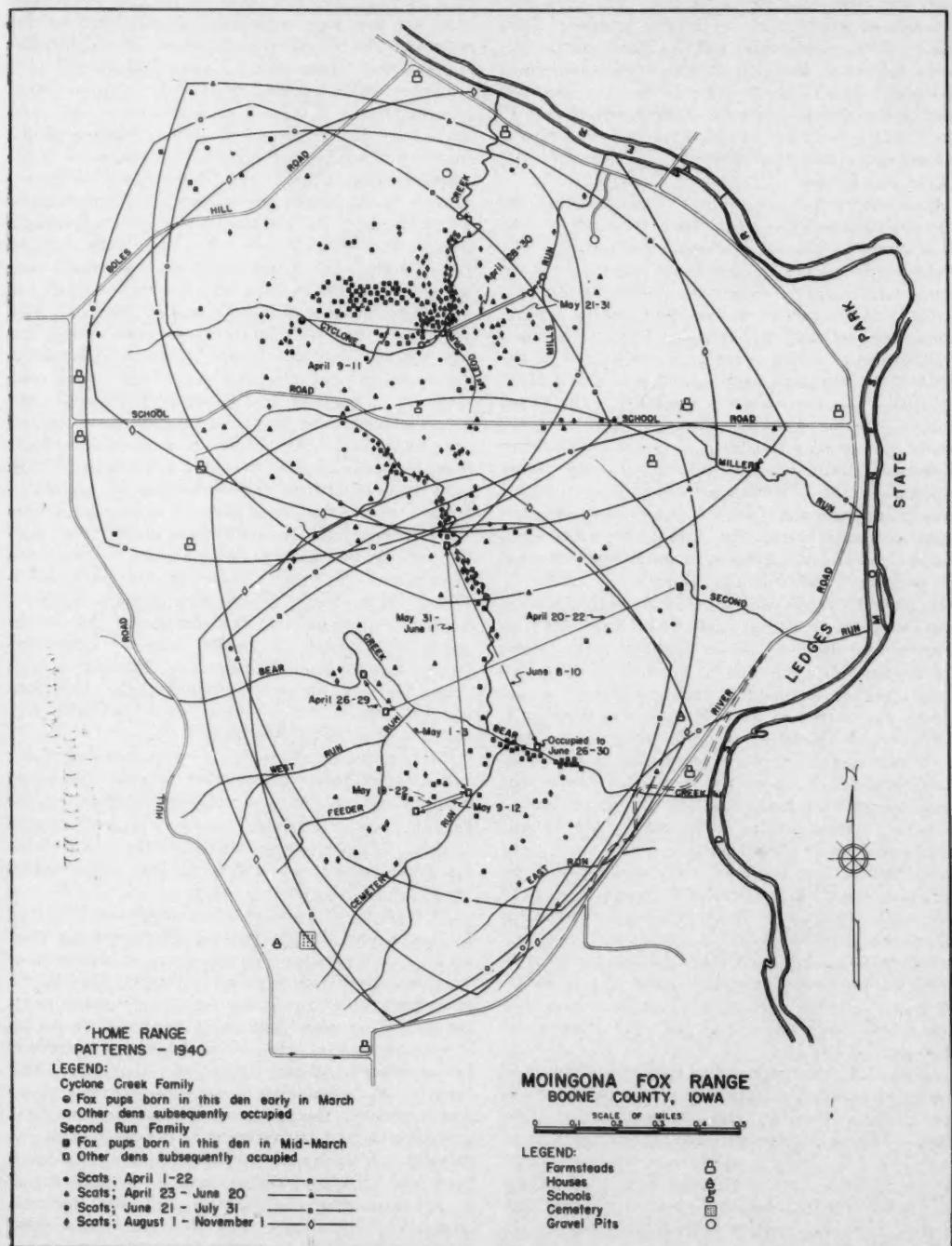


FIG. 17. Den sites, direction and time of movement between dens, scat locations and interpolated home ranges, 1940.

main den. No more were ever seen. The pups continued to occupy these dens until late in June. Their activity then centered on a rallying station in the dry sandy bottom of Polly Creek about 100 yards north of the den. This station continued to be in use until late in September when the family moved out in accompaniment to the coming of some wood-cutting operations in that neighborhood. No other rallying station was located.

After the period June 1 to 7, 1939, in which the young abandoned the dens, they remained in the vicinity of the last den about seven weeks. The rallying station was on a series of sand bars along Bear Creek near the dens, well marked in Fig. 17, by the concentration of seat locality records, and an interpolation of the range occupied during this period is shown also. After August 23 the "sign" of the family definitely shifted northward, and a new rallying station was established in a part of Polly Creek near its junction with Rose Run and on a rounded, closely grazed ridge adjoining to the east. Evidence of family activity was found in this general region until October 12. The young then were approaching seven months of age. If the family ties remained intact and another rallying station was established, it was never found. A home range interpolation for this period is outlined in Fig. 17.

In 1940 the Cyclone Creek family remained much in evidence on the sandy bed of the creek near its junction with McLeod Run, a rallying station which they abandoned in mid-June. Their "sign" was regularly observed, but the new rallying station was not located until early in July when it was discovered on the broad upland ridge north of Cyclone Creek deceptively concealed in the depths of a well-cultivated cornfield. This station is well marked by the locality records of seats collected during the period (Fig. 17). After August 1 the rallying station was back in the closely grazed bottoms including Cyclone Creek, mainly just north of the mouth of McLeod Run, and including the southeast corner of a cornfield to the northwest. The seat locality records for this period show the rallying station by their concentration (Fig. 17). Evidence of the family continued to appear at this station more or less continuously until October 23, after which the "sign" was more widely dispersed. The young were then about 7.5 months of age.

During July the Second Run family centered their activity at a rallying station along the sand bars in Bear Creek immediately east of the mouth of Polly Creek. The usual concentration of seats appeared there (Fig. 17). The unusually heavy rains in August may have forced them off the sand bars. As time did not permit further detailed observations on both families, intensive work was continued only in the Cyclone Creek area and observations in the southern part of the area were limited to regular bi-monthly visits. As a result it was not possible to locate accurately rallying stations that may have been used after the family moved off the Bear Creek sand bars

on July 31. The few inspections indicated that probably one had been established to the south of the upland in the closely grazed pasture between Feeder and Cemetery Runs.

Late in October it was obvious in the "sign" readings that some change in activity and in the social unit was taking place. Ground-concealing fallen leaves and subsequent freezing of the earth made "sign" reading difficult. In addition to covering the ground, the mere presence of the leaves was distracting to thorough inspection, especially when there was enough wind to shift them. The little snow that fell was seldom suited to tracking. Nevertheless it was apparent that the rallying stations were unused, and probably with them had gone most of the family ties. The "sign" that was located was more evenly and more widely dispersed than before. Although no direct evidence of the dispersal of the young was obtained, it was clearly seen by late winter that at least the larger part of the population increment had gone somewhere. The red fox population on a single range was too small to permit the taking of enough individuals to provide significant data on age classification, and even then the transient young from other ranges possibly would have complicated matters. Only two animals were known to have been captured on the area: a male trapped early in December, 1940, and a female shot late in February, 1941. Neither animal was thought to have been young of the year. Errington & Berry (1937) reported the capture, tagging and releasing of two young foxes in the vicinity of their den, which were trapped the following winter 16 and 18 miles distant but in opposite directions.

Contributing in a limited way to knowledge of the movement of foxes in December was the subsequent recovery from a seat of a metal tag inserted into the flesh of a cottontail found on the area on December 3, 1940. The seat was collected two-thirds mile from the place where the cottontail had been located (Fig. 18).

Perhaps the history of the family that occupied the north part of the area in 1940 explains what occurs at this season. The family, probably the same eight animals known to make up the unit until late in May, was in evidence in the region until about October 23. The "sign" gradually became more evenly and more widely scattered and perhaps somewhat less abundant. About December 11 a large male thought not to have been one of the season's young was trapped in the northwest part of the area. On December 17, in unusually good tracking snow averaging eight inches in depth, by following the outermost trails it was possible thoroughly to trace out all of the area then occupied in that part formerly occupied by the family (Fig. 18). This represented the scope of all the movement that occurred between 4:00 p.m., December 16, and 4:00 p.m., December 17. An area of approximately 25 acres was involved in the movements. It was the movement of a single fox, probably a female as evidenced by the method of

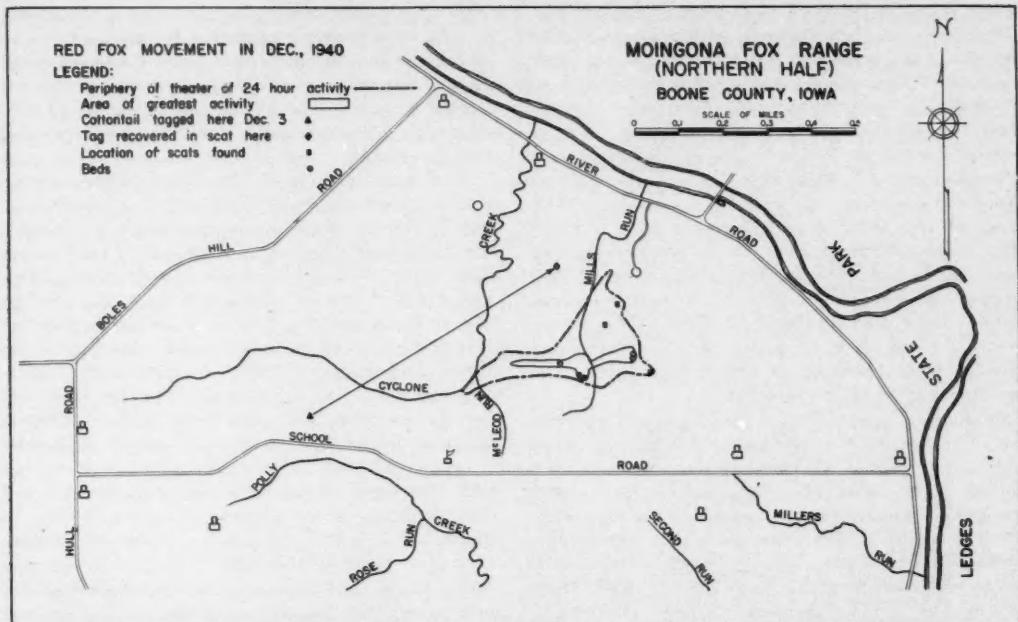


FIG. 18. Scope of activity of one red fox during a 24-hour period. Locality where consumed and place of recovery are also shown for Monel metal tag swallowed by a red fox.

urination. No trails of other foxes crossed the boundaries of the area. Fox "sign" continued to appear in the north part of the area until January.

#### FEEDING BEHAVIOR

##### HUNTING METHODS

Judged from tracks in the snow, stealthy approach was frequently employed by the fox for capturing certain kinds of prey. Cottontails were commonly taken in this manner, usually while resting in forms, and birds too were obtained by stalking. Sometimes the stalk was terminated by a final rush or leap. Occasionally, foxes appeared not to detect prey within easy stalking distance, as fox trails were traced several times within 10 feet of cottontails resting in snowy forms. In each case it was known that the cottontail had been in the form when the fox passed because the fresh snow had not been disturbed.

The stalking technique, usually directed at resting prey, was applied also with little variation to the capture of moving animals, as depicted in a late snow on March 11, 1941. A long-tailed weasel had passed through an open pasture at a moderate speed, 14- to 16-inch leaps, towards a gully in the steep slope immediately southwest of the juncture of Polly and Bear creeks. At the same time a fox had traveled along the base of the slope at a walk or trot, with tracks spaced at 12- to 14-inch intervals. Evidently just as the weasel ascended a slight elevation of the terrain the fox became aware of its presence, because the tracks showed that the fox had stopped and

turned toward that part of the weasel's trail about 40 feet distant. The fox climbed a slight elevation in the ground, again faced the direction of the weasel trail, and then continued at the same pace along the base of the slope. The weasel meanwhile continued on a straight but longer line of travel toward the gully. The stalk was perfectly timed, for the fox caught the weasel without so much as changing gait. The weasel must have been unaware of the danger up to the very end, since there was no change in the spacing of the tracks to indicate that it had changed pace or dodged. The weasel, in white winter pelage, was found where the fox had left it in a snow cache about 100 feet away.

Murie (1936) found that the foxes usually captured cottontails by out-sprinting them in relatively short races. In this study only three such attempts were noted, none successful. These seemed to have failed because of the effectiveness with which the pursued cottontails used escape cover. In one instance escape was made possible by a woven wire fence grown over with grape vines. The fox gave up the chase at the fence even though the cottontail continued on across a 100-foot strip of open field before reaching security in a hole. Another time a fox found that scattered limbs, trimmed from a tree trunk and grown around with hemp, were too great an obstacle. Another cottontail made good its escape by running up a hill through a partly broken over stand of greater ragweed (*Ambrosia trifida*).

As all known successful stalks on cottontails occurred in spaces relatively free of brushy or weedy

ground cover, it appeared that the fox found it difficult to stalk when the obstacles in its path hampered free movement. As the vegetation went down under the frost and snow there was a noticeable movement of cottontails into winter concentrations in brushy gullies and other locations offering cover. Tracks showed that foxes regularly inspected such places of concentration. This was particularly obvious during the deep snow and cold late in January, 1940. Then, at one gully covert drifted full of crusted snow three cottontails were taken by foxes in two days. One animal was captured while it rested in a form in the scant cover offered by the tips of rose bushes (*Rosa blanda*) barely projecting above the heavily crusted snow. Possibly the other two were attacked while browsing on the tips of sumac and rose reaching above the snow.

Some prey, such as mice, were simply snatched out of cover that was inadequate in protection against the jaws of the fox. Foxes were observed hunting in this manner. Apparently when quarry was sensed, the fox paused and raised its tail. The tail was snapped down as the animal gracefully pounced on the prey or its suspected hiding place, and the feet were brought into play to hold, frustrate or sense the movements of the prey. This hunting behavior was detected in snow many times, and sometimes a mouse or evidence of one was found nearby. Here it was seen that the fox made an abrupt turn from the line of travel to leap on a spot as much as 10 feet away. It seems probable that in such cases the fox was attracted by the squeaking of mice in their snow-blanketed, grassy retreats. Note was made of instances in which foxes had thoroughly trampled small areas of dense, grassy cover.

Decayed stumps were torn open for mouse nests, probably of the northern white-footed mouse. Shallow ground nests of mice were pawed open. Perhaps most frequently observed was the digging into mole runways. As the moles did not seem so desirable as food the dead mole with broken skull and mottled fur was often found at the digging. Perhaps the fox may inspect mole runways for other animals that inhabit them occasionally. The willingness of the fox to dig for food was seen in connection with an experiment to determine the response of neighboring turkey vultures to food available at the den. A domestic chicken was placed on the earth outside a fox den that had just been evacuated, and after the vultures had picked it clean a heavy log was rolled over the remains. A visit two days later revealed that foxes had excavated the soil from beneath the log at the point where the chicken had been left. The undigestible remains of the bird did not appear to have repaid the fox for its effort because there was no evidence that any of the parts had been removed.

A single observation was made of a red fox late in summer that leaped from the ground and snapped at a butterfly that flew overhead. Analyses of feces

containing insects seemed to indicate that the foxes lingered on especially productive grounds.

Fruits such as of the service-berry, American plum (*Prunus americana*) and wild black cherry (*Padus virginiana*) were taken from the ground. Gooseberries (*Grossularia* spp.) probably were plucked from the bushes.

Emergencies such as extreme cold left the hunting grounds of the foxes with a supply of carcasses, particularly birds. The fox trails then led to weed patches, fence rows and overhung stream banks where birds often took refuge and sometimes died. During the winter of 1939-40 foxes were noted to have made regular trips along Bear Creek, turning in to inspect every overhung bank that might have offered protection to birds. Feather remains indicated the success of the hunt. It appears then that such carrion foods were located by deliberate examination of locations which past experience showed to be sources of food. Foxes also returned to carrion foods that they had killed on earlier expeditions and some carrion apparently was found by chance.

#### FOOD CACHES

A cache, as here understood, existed whenever food items were at least partly covered with soil or ground litter through the efforts of the fox. The cache usually was made by excavating a hole, depositing the food item therein and pushing the excavated material over it with the nose. Most of the caches were in snow, and in seasons other than winter caches usually were in sand of dry runs. One cache was located in a deep litter of twigs and leaves, and another was found in cultivated soil.

During the course of this study 109 animal food items were located together with unquestionable red fox "sign" (Table A, appendix). A number of these were represented only by bits of fur and sheared feathers that remained after the fox had finished eating. Of fleshy items 20 had been placed in 16 separate caches. The cached items were: meadow mice, 7 (5 complete individuals in one cache, 1 complete individual in a second, and fore quarters only in a third); cottontails, 6 (all entire except for 1 represented by hind quarters and 1 by a hind leg and in separate caches); mole, 1; raccoon, 1 (hind quarters); long-tailed weasel, 1; northern white-footed mouse, 1; white-breasted nuthatch, 1; a strip of cow hide; a piece of hog hide.

Caches were found in every month of the year except May, September and October. While snow was on the ground in winter, 1938-39, four caches were found and in a winter of scarce available food, 1940-41, only a weasel was found in a cache. Of 60 food items that Murie (1936) found along fox trails, 26 were in caches. This frequency of cached food and other evidence presented by Murie indicates that more food was available on the Michigan reserve than on the Moingona Range.

The 34 food items left exposed were: hind quarters and skin from back of a toad (*Bufo americanus*);

a swamp sparrow (*Melospiza georgiana*); head and neck of domestic chicken; an opossum; large short-tailed shrews (*Blarina brevicauda*), 4; small short-tailed shrews (*Cryptotis parva*), 2; moles, 8 entire and only fore quarters of 1; a half-grown mink; meadow mice, 2; white-footed mice, 7; and parts of 5 cottontails, ranging from a single hind leg to an almost complete carcass.

All of the items in caches eventually disappeared, but it was possible to trace the cause of disappearance to foxes in but three instances. This seems to indicate a fair degree of use, considering the difficulty of tracing the fate of carcasses, the competition of other flesh eaters, and the fact that only 11 of the items in caches were among the more frequently eaten fox foods. A complete history was obtained on one cache. On December 26 or 27, 1939, a fox killed a cottontail, ate the fore quarters and deposited the hind quarters in a cache which was located on December 27. A 2.5-inch snow fell during the night, ceasing about 6:00 a.m., December 28. Inspection that afternoon showed that a fox had opened the cache, moved the food and covered it over again. The directness of fox trail to the cache indicated that the fox had not found it necessary to eat about in order to find it. The cache was undisturbed when examined January 1 and 4. On January 5 "sign" showed that a fox had opened the cache and eaten the contents, which cold weather had preserved well. White-footed mice placed in artificial caches under two to three inches of sand on a fox "crossing" in Polly Creek and maintained for two weeks were passed over by foxes frequently, but not dug out. This possibly emphasizes the importance of place memory in relation to return to caches.

Foxes visited items that had been left uncovered. Some items, such as moles, were visited many times though apparently little valued as food, and occasionally foxes left scents and seats. Fox "sign" reappeared where only traces of a former meal persisted and appeared about some dead animals or parts of animals without feeding evidence. The food remains of other predators were inspected by foxes, and possibly some of the scraps were eaten for it seems unlikely that a hungry fox would pass up such materials.

#### UTILIZATION OF FOOD

Never were more than three cottontails known to have been killed during a single night on the Moingona Fox Range. But surplus food was seldom wasted. Particularly in winter when some animal associates found it difficult to obtain food, they utilized fox surplus kills.

Crows were repeatedly flushed from food left by foxes in winter. There is much evidence to indicate that at other times of the year crows keep a close watch on their fox neighbors. Several times cawing crows attracted the observer's attention to foxes that had been started and would have otherwise gone unseen. During the spring, 1940, a tethered female fox

was observed for three days. Cawing crows perched in nearby trees attended this fox for brief periods throughout each day, but none of them was known to have fed on the cottontails with which the fox was supplied.

There was usually a complete economy of the kills, as indicated by this fairly complete case history. At 9:25 a.m., December 29, 1939, the observer was attracted to the center of quadrat V by a small flock of crows that had located a cottontail placed in a snow cache by a fox. The head and left shoulder of the animal were exposed, revealing the absence of the left leg. At about 1:00 p.m. a red-tailed hawk was chased from the carcass; an hour later four magpies were flushed from feeding on the cottontail. Nothing remained except the skull, a section of the vertebral column and three legs all picked clean, at 4:35 p.m. Mouse tracks and droppings were found on the site when examined the following morning. By January 1 the bones had disappeared and only scattered bits of fur remained.

In spring other animals found and fed on the food that foxes brought to the dens for the young. There was never as much food litter on the den sites in the Moingona Fox Range as on other sites visited at the same time, possibly because of greater difficulty in obtaining food. The possible role of the turkey vulture in scavenging on den litter has been described (Scott 1941a). Black-capped chickadees and white-breasted nuthatches were observed pecking at mammal remains outside a den early in spring.

During the summer months ants were seen in large numbers on fox food items. About 20 ants (*Prenolepis imparis*) were collected from a northern white-footed mouse that had been discarded by a fox. Other insects scavenging on food left by foxes were: Diptera, undetermined eggs and larvae; Coleoptera; *Silpha* spp.; and *Necrophorus* spp.

During the summer months insects literally tore the fecal passages to bits. The following insects were taken on passages: Formicidae, several species; Diptera, several species; Coleoptera; *Onthophagus* spp.; *Trox* spp.; and *Aphodius* spp. The ants and flies appeared to feed on the mucus coating while the beetles burrowed into the seat. Undetermined mites and harvestmen (*Liobunum* sp.), late in the summer, were on the passages, presumably feeding on the mucus coating. On two occasions "sign" indicated that small birds had picked seeds out of fox scats.

#### FEEDING TRENDS

##### FOOD ANALYSIS METHODS

In the field only 110 food items for which there was sufficient evidence to permit satisfactory reconstruction of case histories were located (Table A, appendix). Although the method possesses important qualitative values for certain forms of vertebrate prey, it does not lend itself to a suitable quantitative analysis of the foods.

Trends in the diet were investigated by analysis of fecal passages because the large number of feces available made possible a continuous determination of the relative quantities of foods consumed. During the study 1,454 fecal passages were collected and analyzed of which 1,220 were scats of adults and young old enough to have loosened or broken their ties with the dens. Three times this number were found and discarded in the field because of absence of satisfactory "sign" on which to base records. No passages were collected at rearing dens in 1938 and in 1939 only 12 were gathered. With two families on the area in 1940 it was thought advisable to make careful collections of passages at rearing dens, 222 in total. Fecal passages of adult foxes can almost always be distinguished from those of the young foxes still in rearing dens, particularly during the first few weeks after the pups appear outside the dens (Fig. 19). Observations at over 50 dens never resulted in

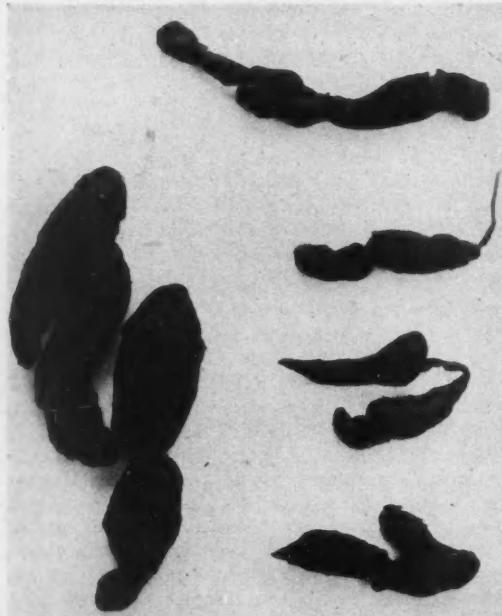


FIG. 19. Fecal passages of red fox cubs about eight or nine weeks of age (right) compared with the passage of an adult (left). About two-thirds natural dimensions.

the detection of adult passages among the smaller ones of the youngsters during the time of rearing in the dens. The 234 passages collected at rearing dens are considered as those of young foxes.

Fecal analysis is uncertain when easily digested foods or those lacking indigestible elements are eaten, and in some instances the utility of the technique may depend on whether or not animals consume significant amounts of such foods. Observations in the field and on caged foxes did not reveal a tendency to feed extensively on such foods, and experimental feeding of caged animals did not indicate that there

was any serious reduction of the identity of the foods through the digestive processes.

The general method of preparing the fecal material for analysis was as follows: Each scat was softened in warm water. The parts of diagnostic significance were separated and cleaned by washing the softened material in a sieve (12 meshes to the inch) over a glass jar; thus, parts that occasionally passed through the sieve were retained for examination. The remaining material was soaked in a glass beaker filled with clear water in which the heavy objects settled out of those that floated. The floating material then was poured by portion into petrie dishes where it was mechanically separated and, except hair, removed with a forceps to a paper blotting towel. The hair left in the petrie dishes was caught in a sieve and removed to the blotting towel as were the heavier parts caught in the glass jar and beaker. Identifications were based on the segregated diagnostic parts.

The relative proportions of the various foods are expressed in percentages of the total number of times each occurred in the collections of fecal passages. By experiment with caged foxes this frequency of occurrence method of analysis was shown to provide a suitable interpretation of the relative quantities of foods consumed (Scott 1941b). The method was refined further by a progressive group treatment of the food items. The sequence is designed so that no group or item may possess greater potential for scoring occurrences in the same passage than those with which it is contrasted. This treatment is extended to include grouping of undetermined and determined items where foods could not be identified beyond a general group. The various divisions of the foods, from major groups to specific items, may be seen in the tables of the Appendix. The percentages are calculated first for the major groups, then for the next largest constituent divisions and so on down to the final items.

The number of occurrences resulting from a specific food appears to vary somewhat in direct proportion to the amount eaten. Experiments (Scott 1941b) with captive animals indicated that on the average one occurrence might be expected for about an ounce of food ingested. Thus, a large meadow mouse averages one to two occurrences, whereas a meal of domestic chicken may result in as many as 15 or more occurrences. Likely, certain small-sized foods when eaten regularly in small amounts would have a frequency much in excess of the actual volume. This would also tend disproportionately to reduce the relative amounts of associated foods commonly taken in large quantities. Hence among the invertebrate foods only the numbers of occurrences are shown in the tables. But in order to demonstrate graphically the trends of the principal invertebrate foods in the diet, percentages were calculated for those items, identified at least to the genus, that occurred over 50 times in the 1,220 scats collected away from rearing dens.

Whenever possible prey remains were classified in one of the three age groups: immature, young and adult. Remains that could be identified as from full-grown animals were listed as adult, remains of half-grown to full-grown animals were indicated as young, and those less than half-grown were noted as immature.

#### GENERAL FEEDING TRENDS

The feeding tendencies of red foxes have been reported for *Vulpes* sp. in southern Wisconsin and Iowa by Errington (1935, 1937), in Minnesota by Hatfield (1939); for *Vulpes fulva* in Michigan by Dearborn (1932), and by Murie (1936), in New York and New England by Hamilton (1935), in part of the Harvard Forest, Petersham, Massachusetts by Hamilton, Hosley & MacGregor (1937) and in Virginia by Nelson (1933); for *Vulpes vulpes* in Russia by Baranovskaja & Kolosov (1935), and in Great Britain by Southern & Watson (1941). The basic feeding tendencies of the red foxes on the Moingona Fox Range were not exceptional to the reports of these investigators.

The foxes here were primarily carnivorous, with substantial quantities of insect and plant foods consumed when available. A bar graph (Fig. 20), based on percentages of total occurrences, shows the relative amounts of foods in the major groups for each of the three years of study. Of these major divisions the invertebrate group is almost wholly of insects.

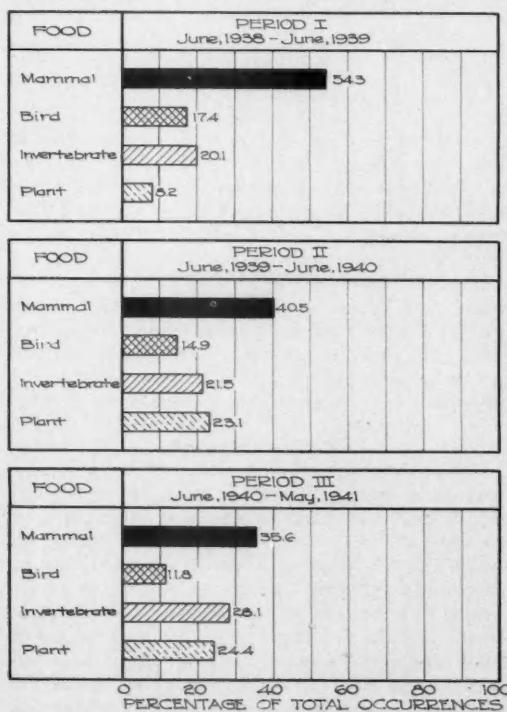


FIG. 20. The annual representations of major food groups in the diet of the red fox.

The cold-blooded vertebrate segregation is not shown in the graph because of its relative unimportance. For convenience in making reference within the text the three years of study are designated as Periods I, II and III, each 12-month period beginning June 1.

Increased representation of a food in the diet does not necessarily reflect a change in its availability. A conveniently available food may become more prominent in the diet simply because some normally easily available food has become difficult to obtain. Frequency of occurrence then should not be considered an unquestionable expression of degree of availability. This emphasizes the importance of investigating definite areas on which it is possible to make continuous intensive observations for correlation with laboratory work.

Availability of foods only occasionally varies so profoundly as to produce a significant modification in the annual pattern of the major food groups. When the annual pattern of the major food groups in Period I is contrasted with Periods II and III (Fig. 20), a pronounced increase in plant representation becomes obvious. This reflects the failure of the local crop of wild fleshy fruits during the summer of 1938. Such a difference in plant occurrences was also reported by Dearborn (1932) who found that fruit remains made up 31.5 percent of the total food in 1930 when the fleshy fruit crop, particularly of service-berry, was enormous, whereas in 1931 when the crop was light and not easily available and when more of the seat collections were made, they made up only 3.6 percent of the remains. Errington (1937) who compared the diet of red foxes in Iowa during the "normal" spring and summer of 1933 with the same seasons in 1934 attributed an increase in the occurrence of certain prey, especially insects, in 1934 to the adverse effects of a summer drought in the latter year.

The progression of the seasons is naturally accompanied by modification in availability of foods. The seasonal trends for each of the three years of study are graphically presented in Fig. 21. The representations of mammal foods are lower in summer and fall than in winter and spring. This does not necessarily reflect a seasonal change in the availability of mammals in general, but to a large extent it is probably a compensatory response to the increased seasonal availability of plant and invertebrate foods. Bird food is usually more prominent in winter and spring diet. The high frequency of bird food in summer of 1938 was the result of an unusual increase in the availability of domestic chicken. Invertebrate foods, almost wholly insects, naturally take on largest proportions in the summer and fall while during winter and spring are of little consequence. Plant foods usually are of greatest importance in summer and fall because of the availability of fleshy fruits in those seasons. It is of interest to note that there was somewhat less plant food in the spring diet than the winter. The most striking seasonal transitions are spring to summer and fall to winter.

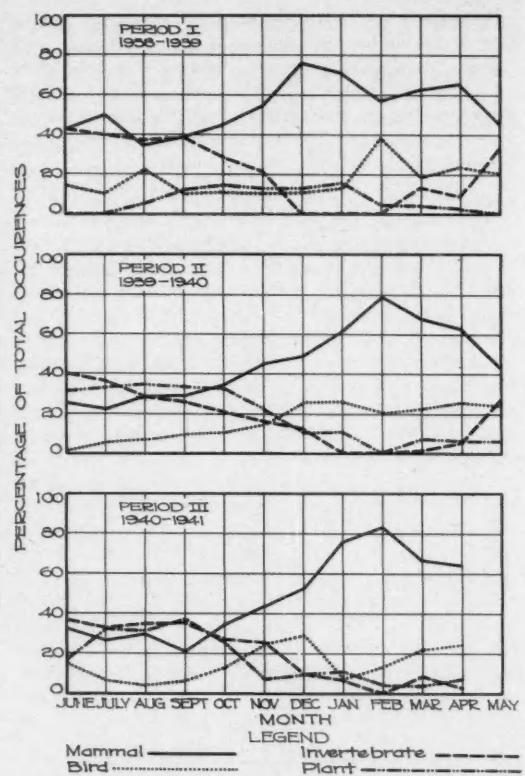
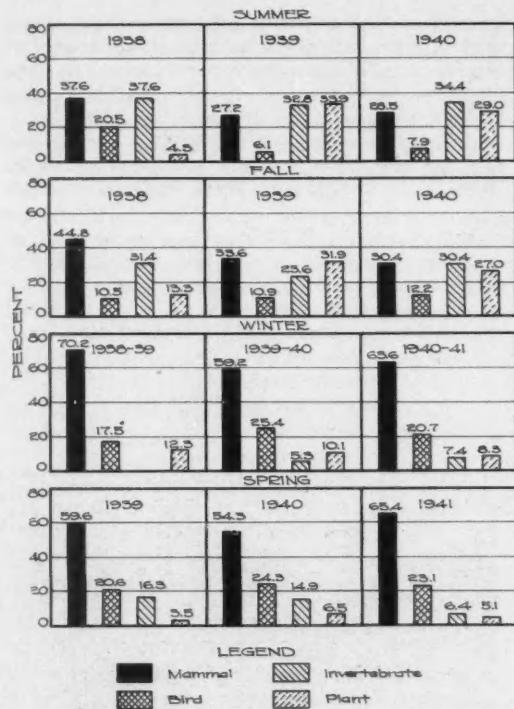


FIG. 21. Seasonal representations of the major food groups in the red fox diet.

In addition to the seasonal trend a comparison of the dietary pattern of similar seasons in each of the three years is also possible. The conditions that govern the general proportions of these major groups of foods in the summer season seem to continue effective, though somewhat modified, into the fall. This may be seen in the similarity of the graphic patterns of the diet in summer and fall of each year (Fig. 21). Although less striking than the spring to summer and fall to winter changes there is an obvious variation in the graphic patterns of the winter and spring diets. A comparison of the three winter and three spring seasons reveals a year to year steadiness in the relative positions of the major food groups in the diet. In order, beginning with the group possessing the greatest percentage of total occurrences, the alignment is consistently mammal, bird, plant and invertebrate in the winter season of each year and mammal, bird, insect and plant in the spring of each year.

The month to month trends in the major groups of foods in the diet are presented in Fig. 22. Most of the month to month changes are simply a reflection of seasonal trends. The abrupt increase in bird consumption in August, 1938, was caused by an unusual availability of domestic chicken. In February, 1939, there is a depression in the proportion of mammal and an increase in bird because during that month a period of extreme cold and snow resulted in the death

of many birds which foxes picked up more readily than less available mammals. Again in November and December, 1940, an increase in birds in the diet reflects the effect of severe weather on bird life.

Although wildlife was not so severely affected on the range by the unseasonal November, 1940, blizzard as elsewhere (Scott & Baskett 1941) there was nevertheless a noticeable decimation, particularly among migrant sparrows. Thus it seems that severe weather greatly modified the availability of birds in the diet, and probably contributed in a large measure to the proportion of birds appearing in winter passages.

#### FOOD PREFERENCES

Within the broad dietary limits of its primarily carnivorous habit, the red fox seems to show food preferences. The positions of the various foods on the scale of preferences are difficult of evaluation, and the bulk of the foods can be classified only as intermediate between two extremes.

Detailed knowledge of the relative availabilities of potential foods is necessary to the segregation of highly desirable items. Among the foods that appeared to be especially preferred in this study was the meadow mouse, and possibly the lemming mouse.

It is easier to discern those foods for which the feeding reaction of the red fox is markedly toward

the negative. Insectivores were regularly left uneaten by the hunting red foxes on the Range. Mammalian predators generally seem to find insectivores distasteful (Barrett-Hamilton 1910-21; Errington, Hamerstrom & Hamerstrom 1940). Few remains of insectivores were found in the many fecal passages and stomachs of red foxes examined during the investigations by Dearborn (1932), Nelson (1933), Hamilton (1935), Errington (1935, 1937), Murie (1936) and others. In Great Britain, Southern & Watson (1941) considered the absence of shrews in their study of the red fox noteworthy. Weasels appeared to be even more distasteful to the red fox than insectivores. In Iowa, Errington (1937) found that weasels occurred 5 times among 1,010 individual food items from 113 dens in 1933 and 14 times among 2,848 items from 200 dens in 1934, whereas none was recorded in 2,110 fecal passages collected about the same dens. Contemporaneous observations on many areas inhabited by foxes indicated that weasels are commonly killed and discarded. On the Moingona area one weasel was known to have been killed and left uneaten while another had been rejected at least in part. In the latter instance the evidence strongly indicated that the fox had discarded the entire animal and that an avian predator had subsequently taken part of it. *Mustela*, identified 3 times in 57 fecal passages collected in September, 1940, was very probably mink taken at a time when there appeared a shortage of vertebrate foods on the area. It was also evident that the foxes did not feed on several dog carcasses that were easily available on the Range.

Carrion seems to bear some relationship to food preferences. As here construed, the term "carrion" applies to all animals that were dead when approached by the feeding fox, irrespective of the state of decay. Within the limits of the usual preferences the fox showed no distaste for those carrion foods not noticeably advanced in decay. About 16 percent of all the vertebrate animals on which the fox fed during the course of the investigation was carrion. Although carrion that was advanced in decay was visited by foxes, on no occasion did they apparently take more than parts little affected. In May, 1940, a young pig which died on a nearby farm was dragged into a gully between Mills Run and Cyclone Creek. The foxes immediately took advantage of this easily available food, but by the time decay was noticeable the "sign" and analysis of the fecal passages indicated that they had ceased to feed on the carcass. Eventually all of the soft parts of the animal sloughed away and only the skeleton remained. Late in December a fox trail was traced to the skeleton from which the end of a humerus had been chewed. Possibly in this some relationship may be seen to the eating of the feet of carrion chickens as described by Errington (1935).

#### INFLUENCE OF AGE ON FEEDING TRENDS

Early in life a fox pup must rely on the parents for food and then in easy stages it assumes the re-

sponsibility of obtaining its own subsistence. It seems logical that young animals should at first begin to take food by sampling everything and rejecting that which proves distasteful or painful (Holmes 1911).

Little or no evidence of contamination by non-food material was detected in the fecal material that was gathered at the den sites in the Moingona area during the first two or three weeks after they began to appear. Thereafter increasing amounts of debris such as leaves, sections of twigs, bark, rotted wood and other non-food items appeared. Perhaps a part of this was caused by feeding of the pups outside the den where there was greater opportunity for contamination with non-food debris. Or likely, some of this resulted from the tendency of the pups to bite and chew at everything within easy reach of the den entrances (Fig. 23).



FIG. 23. Red fox cub estimated to be about eight weeks of age.

Analysis of excreta from about the dens of *Vulpes vulpes* in Russia revealed certain dietary trends that were thought to have been reflections of the growth and development of the cubs (Baranovskia & Kolosov 1935). Something of the feeding trends of red foxes in early life may be more clearly understood through comparison of the kinds and frequencies of foods in the fecal material gathered at the dens (Table C, appendix) with those for droppings collected away from the dens (Table E, appendix). The data that Murie (1936) assembled concerning the food of the red foxes showed appreciably greater frequency of mouse in droppings picked up on trails than in those taken at the dens. There was also markedly greater cottontail and insect representation in the den material than in that from the trails. It may be expected that where cottontails or other large prey are easily available, more of this type of food will be carried to the pups at the dens while such small animals as mice are more likely to be eaten in the fields by the adults. It is also reasonable to expect an increase of insects in the diet of pups beginning to feed on easily captured prey.

The marked cottontail-mouse differential that is evident in a comparison of Murie's (1936) trail and den findings is absent in a similar comparison of the data from the Moingona Fox area. In fact, there seem to be no appreciable differences or tendencies among the specific food items in the den and trail material collected here. It is likely that Murie's findings would have been more nearly approached on the Moingona Fox area had cottontails been as easily available as they apparently were on the George Reserve. The Moingona data does, however, reflect the same general tendencies as observed in Murie's work. A comparison of the percentages of total occurrences for the principal groups of foods detected in fecal passages from the trails with those picked up at dens demonstrates this (Table 1).

TABLE 1. A comparison of the percentages of total occurrences for the principal groups of foods detected in fecal passages collected on the trails (April, 60; May, 58; June, 47) with similar percentages for passages picked up at dens (April, 117; May, 89; June, 16) in 1940.

	MAMMAL		BIRD		INVERTEBRATE		PLANT	
	On trails	At dens	On trails	At dens	On trails	At dens	On trails	At dens
April.....	62.8	72.2	25.5	27.8	5.3	0.0	6.4	0.0
May.....	42.7	41.4	24.0	17.1	27.1	36.2	6.2	5.2
June.....	32.5	38.2	14.6	5.9	36.6	44.1	16.3	11.8

In April, when the pups were most dependent on the adults for food, the remains of mammals and birds were more frequent in the fecal material from the dens than in that gathered away from the dens. At the same time, while limited amounts of invertebrate and plant remains appeared in fecal passages collected on the trails, no evidence of these foods was detected in the fecal passages picked up on the den sites. In May, when the pups were presumably a little less dependent on the adults, the mammal and bird remains were not so frequent in the den material and more frequent in that from the trails. At the same time the invertebrate representations, almost entirely insects, showed an abrupt increase from no determinations in April to 36.2 percent of the total occurrences in May. This May frequency in the den material is 9.1 percent greater than that for the fecal samples collected away from the den sites. Thus the relative proportion of invertebrate foods in the passages from the trails and dens in April are reversed in May. While plant remains did not occur in the den collections in April, they did occur in May but did not surpass the representation for passages picked up on the trails. In June the relative proportion of mammal in the den collections became greater than that for the trails. The data for the June comparison is based on only 16 passages collected at the dens during the first part of the month and therefore is probably not representative of proportions for the month as a whole. The gen-

eral trend continues downward for mammal and bird representations, whereas the invertebrate and plant representations move upward.

A difference is noted in the frequency with which immature cottontails appeared in the fecal passages from the dens as contrasted with those from the trails. In April, when 10.6 percent of all cottontail appearances in the feces from the trails was of immature animals, 19 percent of all cottontail occurrences in fecal material from dens was of the immature age class. In May and June, when 20.8 percent and 37.0 percent, respectively, of all cottontail occurrences were of the immature animals in the trail seats, 46.3 percent and 45.5 percent respectively, of all cottontail occurrences in the den material were represented by immature animals.

Some additional data on the food of the young foxes were obtained. A record was made of all the food items seen at the rearing dens and these are mentioned at appropriate places later in the discussion on the specific food items. In addition, the food contents in the stomach of the young fox found dead on May 31, 1940, in the southern part of the area were: domestic chicken, 75 percent; insects, 15 percent; cottontail, 10 percent. The insects, largely *Phyllophaga*, included some *Gryllus assimilis*, *Scarites*, *Calosoma scrutator* and *Calosoma calidum*. Two of the fecal passages examined contained deciduous red fox teeth, thus identifying them as from young of the year. One collected in mid-July, 1939, contained remains of immature cottontail and a substantial quantity of the following insects: *Gryllus assimilis*, *Harpalus caliginosus*, *Scarites* spp., *Evarthrus colossus*, *Bolboecerasoma farctum* and *Melanoplus* spp. The other tooth-containing dropping was collected in May and contained a large amount of green grass-like leaves together with some pieces of twig, rotted wood and bark.

#### RELATIONSHIP OF HOME RANGE AND DIET

Although studies of foxes in different regions show the same basic feeding tendencies, differences in the kinds and proportions of specific foods are evident, largely because of regional variation in availability. To a lesser extent the nature of the home range environment may be reflected in the diet. This was detected in the feeding trends of the foxes on the Moingona Fox Range, particularly in 1940 when two families occupied the area. A separate analysis (Table D, appendix) was made of the fecal passages found in the interpolated home range of each family in order to allow comparison of the diets. Fecal passages collected in the overlapping parts of the two ranges were not included in these analyses. The relative proportions of remains of specific foods in the fecal passages collected at the dens of the two families were also suitable for comparison (Table C, appendix).

In the material collected away from rearing dens the mammal and invertebrate representations were remarkably similar in the fecal passages on both

home ranges while a tendency toward significant differences was apparent in the frequency of plant and bird remains. The den material compared similarly, with invertebrates and mammals detected to about the same extent on both ranges while bird frequencies were more variable.

There were few differences in the frequencies of specific mammal remains in the fecal passages collected on the two ranges away from dens. At the dens, in April, there were more cottontail occurrences on the north range than on the south range while the reverse was true for meadow mice. In May, representations of cottontail were about the same for the findings on both ranges while remains of meadow mice and white-footed mice were somewhat more frequent on the north range.

Bird remains generally seemed more frequent in the material from the south range. Differences in the representations of birds in seats from the two ranges are unreliable beyond the major group because of the difficulties involved in identifying the material. The only quail remains detected were in passages from the south range, whereas the only pheasant remains identified were in material from the north range. Quail were somewhat evenly distributed over the area, but pheasants were most common on the northern part. In April, bird representations in the fecal passages from the dens of the two families were about the same while a tendency toward greater frequency in seats from the south range was evident in May. As in the trail data pheasant was represented only in the fecal passages from the dens on the north range.

The differences in frequency of occurrences of specific plants in the material from the two ranges were supported by the most definite field data. Gooseberry bushes were evenly distributed over the area. Most of the mulberry (*Morus rubra*) trees accessible to the foxes were on the north range, while the majority of the service-berry trees were on the south range. This distribution was almost perfectly reflected by the frequency of occurrences of the fruits of these plants in the fecal analyses for the two home ranges. During the period, June 20 to July 31, when about twice as many droppings were collected on the north range as on the south range, mulberry occurred only 17 times on the south range and 83 times on the north range. At the same time remains of the fruits of service-berry occurred 13 times in the fecal passages collected on the south range and twice in passages from the north range. These particular differences in the diets of the foxes clearly reveal the feeding limitations imposed upon the animals by their home ranges and serve to indicate the validity of the home range interpolations.

Although insects as a group were about equally represented on the two ranges there were significant differences in occurrences of specific insects. Crickets were generally more common in material from the north range while there was a tendency for May beetles and stag beetles to be more frequent in the

droppings from the south range. The material collected at the dens was remarkably similar except that here, too, crickets were more frequent in the passages from the north range than in those from the south range.

#### SPECIFIC FEEDING TRENDS

This investigation is adapted to study of the inter-relationships between the red fox and the specific foods. The many foods, each differing from the other to some extent in life form, life history, ecology and behavior, provide an illuminating background on which to examine the feeding tendencies of the fox.

#### MAMMALS, MARSUPIALS

Opossum. The opossum was represented in only 3 of the 1,454 fecal passages (Table E, appendix). Because all of these occurred in material collected about the same time in December, 1940, it is likely that only one opossum was involved. Errington (1937) listed a small opossum among the 1,010 food items found about 113 red fox dens in 1933; 2 were among 2,848 items collected at 200 dens in 1934. Opossum did not appear in any of the 2,110 fecal passages collected about these same dens. Opossum does not seem to have been detected in any reported analysis of the fecal passages or stomachs of red foxes, possibly because most of the work has been carried on where the animal is absent or of infrequent occurrence. Opossums were not uncommon on the Moingona area, and because of their apparent vulnerability, a greater representation in the food was expected. Three dead opossums were found on the area as well as several live ones. None of the dead animals had been fed upon by foxes, although one had been killed by a fox and its carcass was known to have been visited at least four times. Food on the area seemed unusually scarce during the winter of 1940-41 and the spring of 1941. During this period the remains of several foods not previously identified in the passages appeared. Perhaps this had some relationship to the occurrence of opossum.

#### INSECTIVORES

Mole. The many mole runways that had been ripped open by foxes with victims occasionally left on the site indicated that the fossorial habit of the mole afforded it little protection when foraging near the soil surface. Of *Talpa europaea* in Great Britain Barrett-Hamilton (1910-21, p. 41) wrote: "Dogs and foxes occasionally dig it out." Still more vulnerable are those moles which further depart from their range of familiarity and venture out on the surface. Two moles were captured by foxes while out of the soil runways burrowing in snow, one on December 28, 1939, and another on March 6, 1939. The total of 10 left uneaten on the trails indicate that moles are distasteful to red foxes. Murie (1936) found 2 prairie moles (*Scalopus aquaticus macrinus*) and 1 star-nosed mole (*Condylura cristata*) on fox trails, whereas only 1 prairie mole was detected in 768

droppings. Also evidence of distaste are the few remains of moles in other American investigations of the fox's food (Errington 1937; Dearborn 1932; Hamilton 1935; Hamilton, Hosley & MacGregor 1937). Southern & Watson (1941) reported *Talpa europaea* in 2 of 40 red fox stomachs examined in Great Britain; the 2 stomachs containing mole were from young foxes.

Mole appeared in 32 of 1,454 fecal passages examined (Tables C, E, appendix). In August, 1938, mole appeared in 3 of 28 fecal passages analyzed; this was 2.6 percent of the total food occurrences for the month. With only one occurrence (0.5%) in September and another (1.0%) in December, mole was of little dietary consequence in 1939. In 1940 the frequency of mole occurrence was relatively high and somewhat persistent, primarily reflecting an increase of moles on the Range. The trend began in March with 1 occurrence (1.5%) and 2 (1.6%) in April. In May there was 1 occurrence in 49 passages collected at rearing dens of the Cyclone Creek family during the period May 21 to 30; on May 24 a mole was recorded among the food items observed at the dens of this same family. In June there were 2 appearances of mole in 16 passages collected from Den No. 6 of the Second Run family. Among the passages collected away from rearing dens mole was identified 4 times (2.8%) in the 47 passages for June; in 127 passages collected in July mole continued upward with 15 appearances (3.9%). The percentage of total food occurrences for mammal during that month was 26.5 percent, and among the mammal foods mole was exceeded in relative proportion only by cottontail (11.1%). The occurrence of mole declined to 2 in August. Further emphasizing the proportionately high frequency of mole in 1940 is the fact that 5 of the 10 moles left behind by foxes were observed in 1940; 5 were located on July 3, 6 and 22, September 10 and November 7, respectively. Possibly related to the decline of mole occurrence in August was the unusually heavy precipitation which from July 28 to August 31 amounted to 17.44 inches. June and most of July were dry as was August in 1938 (Fig. 2).

It seems then that despite an apparent distastefulness, fox predation on moles generally tended to follow their relative abundance.

Little Short-tailed Shrew. The little short-tailed shrew (*Cryptotis parva*) appeared 16 times in the 1,220 fecal passages collected away from rearing dens (Table E, appendix). It was not identified in any of the 234 passages collected at the dens. On two occasions it was noted as having been left behind by foxes, once on July 21, 1939, and again on July 6, 1940. Murie (1936) observed 4 individuals left on fox trails and recorded the species only once in 768 passages collected during the period of observation. These data lend further evidence to the general distaste of foxes for insectivores.

Concerning this little short-tailed shrew Lyon (1936, p. 46) wrote: "It is not a common animal and specimens in collections are not numerous." Extensive collecting of small mammals in Iowa shows that the statement need not be further qualified here except that during the summer and fall of 1938, the species seemed uncommonly numerous on the Mingoona area. Several individuals were found dead in the field with no relationship to fox "sign." Considering the usual numbers and small size of the animal these observations seemed reflective of local abundance. Although many traps for small mammals were operated on and off the Range only one specimen of this small shrew was captured in the traps; and that was taken on the Range in summer, 1938. The frequency of occurrence tended to follow the population. In 5 passages collected in July the little short-tailed shrew appeared once; in August 3 (2.6%) were identified in 28 passages. The trend continues upward in September when the occurrences totaled 6 (6.1%) in 19 passages. None was recorded for October and the trend terminated with 2 (4.7%) occurrences for 17 examinations in November. The fox predation on *Cryptotis parva* here seems to reflect the same response to a relatively high population as that suspected by Davis (1938) for barn owls in Texas.

The little short-tailed shrew did not again occur with unusual frequency. There was a single identification (1.5%) in 32 passages for January, 1939; single occurrences were also recorded for October, 1940 (0.6%), and for January (2.2%) and March (1.4%), 1941.

Large Short-tailed Shrew. Although Murie (1936) located 10 large short-tailed shrews (*Blarina brevicauda*) along fox trails none was identified in the 768 passages collected during the same period. Of this species Lyon (1936, p. 49) wrote: "When the animals are fully in heat all the sweat gland tubules are secreting. A musky odor is given off which apparently renders the animal more or less distasteful to carnivorous beasts." Dearborn (1932), Hamilton (1935), and Hamilton, Hosley & MacGregor (1937) found but few of these shrews in the feces and stomachs examined.

The results of the present investigation were not exceptional. The large short-tailed shrew occurred only 7 times in the 1,220 fecal passages collected away from rearing dens (Table E, appendix). It appeared once in 49 fecal passages picked up at the dens of the Cyclone Creek family for the period May 21-30, 1940 (Table C, appendix). Four individuals were found where they had been left behind by foxes. This shrew never appeared to be particularly common on the Range; of 83 small mammals trapped in 1938 it was taken only once; it made up less than 1 percent of the total number of small mammals trapped on the quadrats in 1939 and in 1940 was not taken at all in the quadrats but made up 1.6 percent of all those trapped off the quadrats.

## CARNIVORES

The literature bears evidence that carnivores are not commonly eaten by red foxes. This continued true for the foxes on the Moingona Fox Range.

Raccoon. Raccoon was represented twice in 1,454 fecal passages, once in December, 1940, and again in April, 1941 (Table E, appendix). Several raccoon carcasses were located on the range where they had been left after being pelted by hunters. One of these was left on a section of dry run frequently traveled by foxes; tracks indicated that the foxes had not so much as paused to inspect the animal. On April 27, 1940, the hind quarters of a raccoon were found where a fox had placed it in a cache near the juncture of Polly and Bear creeks.

Mustelid. Mustela, probably mink, was detected 3 times in 57 fecal passages for September, 1940 (Table E, appendix). On June 22, 1940, an immature mink was found where it had been dropped by a fox on the upper reaches of Mills Run. Errington (1937) recorded one mink among 3,858 food items collected about dens in 1933 and 1934.

Striped Skunk. Striped skunk appears to be relatively more tasteful than weasel to the red fox. A few occurrences of this skunk have been reported in the red fox diet (Dearborn 1932; Hamilton 1935; Murie 1936; Errington 1937). In this investigation striped skunk was detected once, in January, 1941 (Table E, appendix). Evidence of this skunk was most common during the last year of study; three individuals were observed during regular work in the field on a single day in April, 1941. It seems reasonable to expect some strife between the red fox and striped skunk resulting from den rights. On several occasions skunks were known to have occupied dens immediately previous to fox inhabitation, and in the fall skunks often moved into dens that had been occupied by foxes during the spring and early summer. Intensive observations of the dens on the area revealed a rather general use of the dens by many animals. The classification of a ground den as that of a specific species could only be temporarily applied because of the changing occupants and in winter the dens were often used by several species at the same time.

Common Badger. The common badger was never known to hold residence long on the Range, but its remains were identified twice in the material examined (Table E, appendix), once in December, 1939, and again in October, 1940. Local farmers usually took control measures against the few badgers that wandered into the Range from the adjacent prairie lands. This was done to limit the excavation of dangerous holes in the pastures and hayfields on the comparatively level upland and terraces. A live active badger would appear to be a formidable adversary for the red fox. Of course, a fox might easily utilize a badger carcass; a badger in hibernation might also be taken.

Canidae. A substantial amount of undetermined Canidae was identified in 1 of the 21 fecal passages

collected for the period April 7 to 20-22, 1940, at the natal den of the Second Run family (Table C, appendix). So far as was known domestic dog was not available at the time. It is possible that the representation resulted from intra-litter strife terminating in the killing and eating of one of the pups. This does not appear to be uncommon among the litter mates of captive red foxes. The evidence strongly indicated that the dead pup from the Second Run family located on May 31 had been attacked by litter mates, possibly after having been injured by rifle shot.

As a whole, carnivore representation in the diet was more frequent during the last eight months of the investigation. Staple vertebrate foods seemed relatively less available during that period than at any other time. Possibly this is reflected in the emphasis on carnivores in the diet.

## RODENTS (FIG. 24)

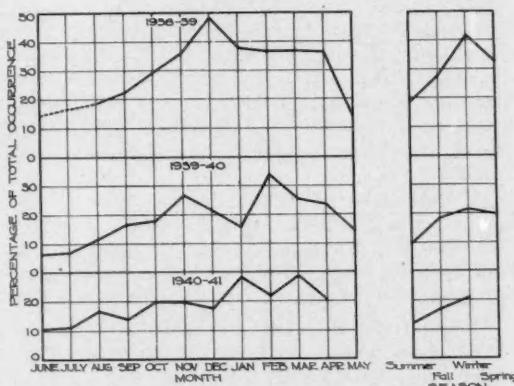


FIG. 24. Monthly trend of rodent representations. A broken line was used where the number of fecal samples was thought inadequate.

Woodchuck. Remains of woodchucks were identified in 7 of the fecal passages examined (Table E, appendix). A single occurrence, in February, 1940, must have been for an animal discovered in hibernation and the foxes are actively preparing dens for the young at this time. Probably all of the dens used by foxes on the Moingona Range were first dug by woodchucks, and these animals are often seen at dens previously or subsequently used by foxes. The woodchucks on the Range generally appeared to come out of hibernation in March; the earliest sight record was March 14, 1939. The latter animal was seen at the mouth of a den occupied for a short time the previous year by a family of foxes. It had not yet ventured from the den as was attested by the tracks. The first small woodchucks usually were observed around dens late in May and the remains of an immature (about one-fourth grown) woodchuck were identified in one of the 58 fecal passages collected in May, 1940. It is possible that these remains were from one of two immature animals

killed in steel traps on May 21 and 22 by a local farmer undertaking control measures. In June, 1940, woodchuck was identified 3 times in 47 passages; the remains in 1 were of an immature animal while the age of the others could not be determined. Red fox pressure on partly grown woodchucks was emphasized in Errington's (1937) findings at dens in spring and early summer. Of 1,010 food items at dens in 1933, 4 were woodchucks, all "young" and 8 woodchucks among 2,848 food items at dens in 1934 also were classified as "young." A single occurrence of woodchuck in 1,175 fecal passages collected at dens in 1933 and 5 occurrences in 935 passages for 1934 were also indicated as "young." Hamilton (1935) reported over 33 woodchucks at 15 red fox dens in New York and New England, a greater number of individuals than for any other species listed. The only occurrence of woodchuck in the 768 passages collected by Murie (1936) during his late winter, spring and early summer studies came in May. It occurred twice in 131 late summer passages from New England (Hamilton, Hosley & MacGregor 1937). On the Moingona area woodchuck was identified twice in 30 fecal passages for November, 1940. In New England woodchuck was reported twice in 66 stomachs taken in fall and winter (Hamilton 1935). Hatfield (1939) found it once in 29 stomachs collected in winter.

All appearances of woodchuck noted in this investigation were for 1940. If the numbers of direct observations on live animals reflect population levels then woodchucks were slightly more numerous during summer of 1940 than in summers, 1938 and 1939.

Ground Squirrel. The thirteen-striped ground squirrel has become established in the uncultivated clearings on the Moingona Fox Range. So little was seen of Franklin's ground squirrel (*Citellus franklini*) that nothing can be said of its status except that it is present on the area. It is logical to expect these squirrels to be less frequently taken by red foxes in winter because of their hibernation from about November to April, and the data support this expectation. Errington (1935) found the thirteen-striped ground squirrel in 2 out of 40 red fox stomachs taken in Iowa in winter. In this study there was one occurrence in December, 1938. By far the most of the ground squirrels are captured during the warmer months. Only rabbits and mice exceeded the occurrences of the "ground squirrels" reported in Errington's (1937) spring and early summer studies. It was detected in 7 of 233 den droppings according to Murie's (1936) Table I analysis. There is only one record of a ground squirrel, the thirteen-striped ground squirrel, for spring on the area; this occurred in 24 fecal passages collected at Den No. 4 of the Cyclone Creek family for the period, May 7-21 (Table C, appendix). Franklin's ground squirrel appeared 3 times, in October, 1938, in August and in November, 1940, respectively (Table E, appendix). The deeply worn molariform teeth of the August representation indicated a very old adult. The

thirteen-striped ground squirrel was detected 3 times in September material, twice in 1938 and once in 1939, and 4 times in 127 passages for July and 2 times in 43 for August, 1940.

Chipmunk. The gray eastern chipmunk is largely established on the wooded slope. These ground-dwelling (Howell 1929) squirrels rarely climb trees and usually remain within easy reach of their burrows. They are wholly diurnal with greatest activity in early morning and late afternoon (Burt 1940). The animals usually disappeared to hibernate late in November and were not known to reappear until March. Chipmunk remains were not listed in the winter stomach analyses reported by Hamilton (1935), Hatfield (1939) and Errington (1935). The earliest and latest occurrences of chipmunk remains were 1 in 50 passages for March, 1939, and 1 in 17 for November, 1938 (Table E, appendix). It was not listed in the spring and early summer studies of Errington (1937). On this area it occurred 2 times in 13 passages gathered about the natal den of the Cyclone Creek family for the period, April 5 to 9-11. During the period, May 7 to 21, 24 passages were collected at Den No. 4 of this family, and chipmunk was detected once in the material (Table C, appendix). Even though the Lyster chipmunk (*Tamias striatus lysteri*) was present on the George Reserve, Murie (1936) did not find it to have been eaten or killed by red foxes during his late winter, spring and early summer observations.

The greatest frequency of chipmunk occurred in passages collected in summer and early fall (Table E, appendix). Two (0.7%) appearances for August and 3 (1.1%) for September were recorded in 1939. Chipmunk persistently appeared in passages from summer and early fall in 1940. This 1940 chipmunk trend follows: June, 3 (1.7%); July, 5 (1.1%); August, 4 (2.5%); September, 8 (3.7%); and October, 1 (0.4%). According to Burt's (1940) data the movements of the Lyster chipmunk on the George Reserve are confined to young animals and adult males. It seems reasonable to expect these moving animals, particularly the inexperienced youngsters, to be more easily captured than well-established individuals. The chipmunk dispersal is correlated in time with the spring and early fall emphasis on chipmunk remains in the fecal material. The parts in two passages, one in June and another in September, could be identified as belonging to young chipmunks. The molariform teeth in 6 of the chipmunk determinations (2 for August, 3 for September and 1 for October) had been deeply worn, like those of very old adults.

Fox squirrel. A tendency for predation to follow population levels was strikingly demonstrated in the predator-prey relationship of the red fox and fox squirrel. Spot counts begun in the summer of 1938 were abandoned because there were so few fox squirrels on the Range that figures could not be obtained on which to base calculations. In the first year of study, Period I, fox squirrel remains were detected

but 3 times (0.3%) (Table E, appendix). All of these occurred in April, 1939, and possibly represent one individual. Errington (1937) reported 0.5 percent of the 3,858 food items about dens in 1933 and 1934 to be fox squirrel, and in 2,110 fecal passages from about the same dens this squirrel was identified but once. Also working within the geographic range of the fox squirrel Dearborn (1932) found it but "sparsely represented" in the red fox diet, and Hatfield (1939) detected no evidence of it among the foods. It occurred 3 times in the 768 droppings examined by Murie (1936), and 4 individuals were found on trails where they had been left by foxes.

The findings for Periods II and III on the Moingona area showed an increased frequency of fox squirrel remains in the fecal material (Table E, appendix). Although no counts were attempted, fox squirrels were obviously more numerous in Period II than they had been in Period I. Reflecting this increase were the 14 (0.7%) occurrences during Period II; the percentage of total food occurrences had more than doubled. The fox squirrel population continued upward and their increased numbers became so noticeable that a spot count was attempted in December, 1940. As a result of the counts the population was estimated to be about one animal to three acres throughout the area. At the same time cottontails showed a population of about one individual to seven acres, a little less than half the estimated fox squirrel density. The increased population level was again reflected in the number of times fox squirrel remains appeared; in Period III there were 24 (1.3%) occurrences. The percentage of total food occurrences, 1.3 percent, had again about doubled that of the previous year of study.

**Flying Squirrel.** Flying squirrel (*Glaucomys volans*) was detected only twice in fecal passages (Table E, appendix). Flying squirrel remains were found in 1 of 11 red fox stomachs taken between December 14, 1931 and February 3, 1932 in Wisconsin (Errington 1935).

**Mice.** The systematic trapping of mice showed that they were greatly disturbed by agricultural operations. Such activities as close grazing, burning, plowing, cultivating and mowing largely resulted in disappearance of the mice inhabiting areas where these practices were undertaken. Often only fence rows grown up to grasses and weeds remained habitable to the field-dwelling mice. Those farming practices that greatly disturbed the land were most intensively carried out during May, June and July. By August the corn has been "laid by" and the small grains have been harvested; thereafter suitable mouse habitat developed rapidly in fields where these crops had been planted. It appears logical to expect mice that have been evicted from familiar range or caused to occupy a greatly modified habitat could be more easily captured by their enemies. At least it has been found true for muskrats (Errington 1939). That mice were affected similarly by agricultural operations was not evident in the fox feeding trends,

possibly because of the effect of the seasonably available fruit and insects. Fox pressure on mice was greatest in late fall, winter and early spring, not only on mice in general, but also on each species.

The data permit an attempt at comparison of the relative proportions of mice taken in traps in the field with the relative proportions of mice in the fecal passages. The records from systematic trapping on the area include the number of individuals of each species taken during definite periods. As the number of occurrences in the fecal passages more accurately reflect size of prey than numbers of individuals (Scott 1941b), it is necessary to correct the field data for size. With average weights of adults as a basis for calculation, the following correction factors seem to make the necessary allowances: house mouse, 1X; harvest, 1X; white-footed mouse, 1.5X; lemming mouse, 2X; and meadow mouse, 3X. One hundred traps during October, 1938, in each of three cover types, fallow field, maple-linden woods and brushy second growth, took 71 white-footed mice, 7 meadow mice and 4 house mice. Corrected for size the proportion of October mice would then be: white-footed mice, 86; meadow mice, 21; and house mice 4. The percentage of the total of the corrected figures may be calculated: white-footed mice, 77 percent; meadow mice, 20 percent; and house mice, 3 percent. By contrast the percentages of total occurrences for mice in the fecal passages were: white-footed mice, 36 percent; meadow mice, 55 percent; and lemming mouse, 9 percent. Similar comparisons have been made for the trapping records and fecal analyses of 1939 and 1940 (Table 2). The differences, even with allowances for error in sampling, are marked and uniform. There is little here that suggests response to population level. Instead specific variation in vulnerability and preferences seem evident.

The trapping records are thought to give a fairly accurate picture of species composition, which is borne out by extent of habitat alone. Trapping throughout the area showed that lemming mice and meadow mice were largely restricted to the few undisturbed grassy areas. This also seemed true for the other field-dwelling forms, such as the Baird white-footed mouse and prairie harvest mouse, except that these species appeared to move more readily into fields where farming operations had been terminated for the season. The forest habitat of the northern white-footed mouse, the most abundant mouse species on the area, was extensive and comparatively undisturbed. In Table 2 the 1940 comparison for May shows remarkable agreement for species composition in the traps and in the fecal passages where all of the trapping was done along a grassy fence row rather than on a bisect through all the representative cover types.

**Prairie Harvest Mouse.** It seems logical that the prairie harvest mouse would be readily captured by red foxes. For the most part harvest mice (*Reithrodontomys spp.*) live on the surface of the ground and even construct nests there, occasionally building

TABLE 2. A comparison of the relative percentage proportions of mice taken in traps on the quadrats and at other localities on the area with the relative proportions of mice occurring in the fecal passages in 1939 and 1940.

	<i>Reithrodontomys megalotis</i>		<i>Peromyscus</i>		<i>Synaptomys cooperi</i>		<i>Microtus</i>		<i>Mus musculus</i>	
	1939	1940	1939	1940	1939	1940	1939	1940	1939	1940
	April									
In passages	4	...	30	...	9	...	57	...	...	...
In traps:										
Quadrats	5	...	95	...	...	...	...	...	...	...
May										
In passages	...	14	...	32	33	4	67	50	...	...
In traps:										
Grassy fence										
rows	15	...	34	...	...	...	51	...	...	...
Quadrats	...	100	...	...	...	...	...	...	...	...
June										
In passages	...	38	33	...	...	50	67	12	...	...
In traps:										
General	14	...	86	...	...	...	...	...	...	...
Quadrats	1	89	94	...	...	...	3	11	2	...
July										
In passages	...	4	50	34	...	10	50	52	...	...
In traps:										
General	2	...	88	...	...	...	8	...	2	...
Quadrats	2	100	93	...	...	...	4	...	1	...
August										
In passages	...	24	30	14	...	62	70	...	...	...
In traps:										
General	...	97	...	2	...	...	...	...	1	...
Quadrats	...	96	94	...	...	...	2	4	4	...
September										
In passages	...	5	22	20	3	5	75	70	...	...
In traps:										
Quadrats	...	96	99	...	...	...	...	4	1	...
October										
In passages	...	24	...	13	...	61	...	2	...	...
In traps:										
Quadrats	4	...	92	...	...	4	...	...	...	...

them above the ground in supporting vegetation (Davis 1939). They are not as abundant as most mice (Anthony 1928) and this is verified by the infrequency of the prairie harvest mouse in traps (Table 2) on the Moingona area. These mice seemed to occur in groups for where one was taken in the traps several more could be expected. The "waves" in the feeding trend may result from locating and feeding in limited areas where the species was present. The seasonal curve (Fig. 25), showing a grad-

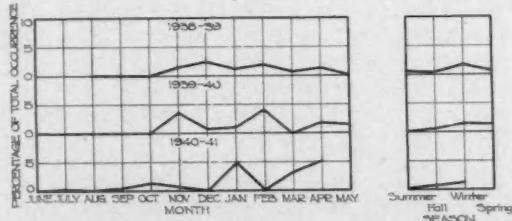


FIG. 25. Monthly trend of prairie harvest mouse representations.

ual rise from a summer low through fall to a winter high followed by a spring depression, seems typical for feeding trends on mice generally in this investigation.

White-footed Mice. As previously mentioned, the northern white-footed mouse and the Baird white-footed mouse are present on the Moingona Fox Range. Mice were trapped on the quadrats from April to October, inclusively, in 1939; 78 percent of the white-footed mice taken were of the northern form and 22 percent were of the Baird form. In 4 months, June, July, August, and September, 1940, 69 percent of the white-footed mice was northern white-footed mice and 31 percent was Baird white-footed mice. This relative difference in numbers for the two species is manifestly the result of habitat restrictions. The woods habitat of the northern white-footed mouse is considerably greater in extent than that of the Baird white-footed mouse. In a discussion of the factors affecting the distribution of these two mice, Dice (1922, p. 30) wrote: "The habitat limitations of those forms is very marked, and, though there is a slight amount of overlapping on the border between the forest and the prairie, the prairie species are not found in the forest nor the forest form on the prairies." This was obvious in the trapping records; only the northern white-footed mouse was taken in the wooded quadrats I, II and VII (Fig. 13). On the other quadrats both species were taken, and Baird's form was particularly evident in the open fields of quadrats IV, V and X. Quadrat IX, in a closely grazed pasture, may be excepted, for no mice were taken there at any time.

Unfortunately it was not found advisable to attempt identification of white-footed mouse remains in the fecal material beyond the genus. If the remains could have been identified to the species with accuracy, something might have been learned of the effect of habitat differences on predation by contrasting the results for these two closely related forms of mice.

The trend of white-footed mice in the diet was generally similar to that of the other mice in that there was a summer low with a gradual increase through fall to winter with a decrease in late spring (Fig. 26).

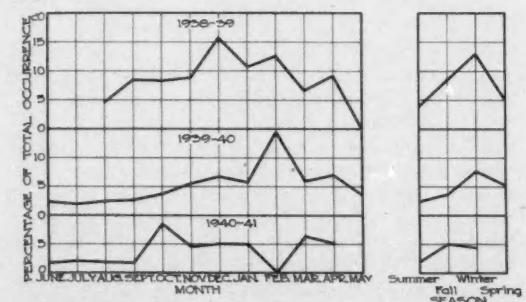


FIG. 26. Monthly trend of white-footed mouse representations.

Though proportionately less abundant than white-footed mice as attested by the trapping records, meadow mice nevertheless regularly occurred a greater number of times in the fecal material than did white-footed mice. The occurrence of white-footed mice exceeded that of meadow mice in only three months, January, February and October of 1940. A fairly deep and continuous blanket of snow was on the ground during January and February (Fig. 14), and this seemed to bear some relationship to the change in the usual position of the two forms as regards number of occurrences in the fecal material. During this period the white-footed mouse appeared more active above the snow than the meadow mouse which remained largely in intricate tunnels beneath the snow. It is possible, too, that the daily rhythm of activity of the white-footed mouse (*Peromyscus leucopus*) might be modified by deep snow (Behney 1936). Therefore, the white-footed mouse should have been more easily available than the meadow mouse during this period. Although the differences in behavior resulting from deep snow are likely to be more evident in the feeding of an avian predator (Hendrickson & Swan 1938), it nevertheless seemed to be of significance to the effectiveness of hunting foxes. The cause of change in relative position for the two species in October could be associated with no specific event.

There were sufficient trapping records for northern white-footed mice to permit estimation of their numbers to the acre for the quadrats as a whole in 1939 and 1940 (Table 3). For this species the population

TABLE 3. Average number of northern white-footed mice to the acre on the quadrats in 1939 and 1940.

Year	April	May	June	July	Aug.	Sept.	Oct.
1939 <sup>1</sup> ....	0.26	....	0.22	0.39	0.78	0.65	1.30
1940 <sup>2</sup> ....	....	....	1.66	1.19	2.45	1.23	....

<sup>1</sup>Because of the agricultural operations and the nearness of denning foxes only three quadrats were trapped in May; the records were not considered extensive enough to permit estimation of the population.

<sup>2</sup>Quadrats not trapped in April, May and October.

level in 1940 was markedly above that of 1939 and the population of Baird white-footed mice was also higher in 1940. There are, however, no evident responses in the diet of the red fox to these greater numbers.

A severe warble fly infestation in the northern white-footed mice on the Moingona Fox Range was reported by Scott & Snead (1942) for the warm weather months of 1939 and 1940. A certain awkwardness was observed in parasitized mice which might have rendered the animals more subject to predation. Nothing was observed in the feeding trends of the fox to support this; but some evidence that parasitized northern white-footed mice were taken by foxes was obtained. In one fecal passage the remains of a northern white-footed mouse accompanied a warble fly larva. In an instance on September 26, 1939, an infested northern white-footed mouse was

found where it had been dropped on the dry sand of Polly Creek.

Lemming Mouse. The lemming mouse appeared to be readily taken by red foxes. Murie (1936) reported a high frequency of the remains of the Cooper lemming mouse (*Synaptomys c. cooperi*) in fecal material, 127 in 535 droppings gathered away from dens and 5 in 233 picked up at a den. In this study the Goss lemming mouse (*Synaptomys cooperi gossi*) was represented in 53 of 1,220 droppings not on den sites and in 5 of 234 found about the dens (Tables C, E, appendix). The feeding trend (Fig. 27) appears

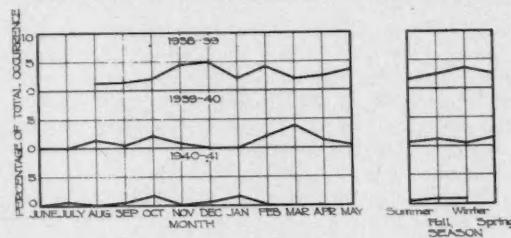


FIG. 27. Monthly trend of lemming mouse representations.

to take the same direction as those of other mice, being generally lower during the warm weather months and higher in the cold weather months. There was a striking year to year change in relative proportion of lemming mouse in the red fox diet (Fig. 27). The percentage of total occurrences for the 3 years of study were: Period I, 2.6; Period II, 1.0; and Period III, 0.5. Though it is highly probable that this year to year decrease in frequency of occurrences is caused by a lowering of the population levels, the lemming mouse was so scarce in the traps that nothing could be learned of its status.

Meadow Mice. As already brought out in the description of the area the Pennsylvania meadow mouse and the prairie meadow mouse were both present. The former apparently limited itself largely to the bottomland fields and the latter shared the better-drained fields of the upland with the Baird white-footed mouse. Meadow mouse remains in the fecal material were identified only to the genus. In 81 fecal samples the molariform teeth were in position and in such condition as to allow examination of the characteristic configuration of the enamel. The teeth in 77 were those of the prairie meadow mouse and only 4 were of the Pennsylvania meadow mouse. Here again habitat restrictions are apparent, for well-drained fields are much greater in extent than moist low-lying fields on the area.

A general lowering of the population level for meadow mice seemed evident in field "sign" and in the trapping records, few though they may be, for the three years' study. Meadow mouse representation in the fecal samples steadily declined during the study as the percentages of total occurrences show: Period I, 15.4; Period II, 7.3; and Period III, 5.9. This decrease in frequency is also manifest in a com-

parison of the seasons showing that the year to year decrease was not brought about by some temporary environmental restriction (Table 4).

TABLE 4. Seasonal percentages of total occurrences for meadow mice.

	Period I	Period II	Period III
Summer.....	9.7	4.7	3.5
Fall.....	12.3	9.9	6.4
Winter.....	19.7	7.3	10.3
Spring.....	18.0	7.5	12.7

The winter of Period II was characterized by deeper snow than usual (Fig. 14). The general downward trend of meadow mouse in the fecal material quickened for that season, probably because of the protective blanket of snow and ice over the runways. Evidence of meadow mice in the fields seemed to be increasing in the spring of 1941.

Meadow mice show a trend (Fig. 28) in the red

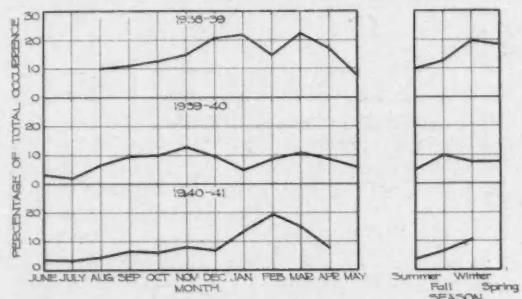


FIG. 28. Monthly trend of meadow mouse representations.

fox diet like that for the other mice. The occurrences are more frequent during the cold weather months than in the warm weather months. Even during the fruit shortage in the summer of 1938 fewer were taken than at any other season. According to Southern & Watson (1941), Chirkova found that voles (*Microtus*) were taken most abundantly by the red fox (*Vulpes vulpes*) in winter, except when especially heavy snow made hunting difficult. Murie's (1936) data also showed that the frequency of meadow mice in the diet of the red fox declined as warm weather approached.

The meadow mouse is thought to be highly vulnerable to foxes (Murie 1936, Hamilton 1935). Its frequent appearance in the diet certainly does nothing to detract from this logic. In this study it was consistently outranked in importance among the mammals only by cottontail. Murie (1936) found it in 109 of 535 droppings picked up away from dens and in 10 out of 233 collected at dens. Errington (1935) identified it in 515 out of 1,175 fecal samples collected at dens. It is equally common in the reports of other workers.

At the same fox dens which Errington (1935) reported meadow mouse in 515 out of 1,175 fecal

samples only 6 meadow mice were among the food debris and this, when contrasted with the 55 white-footed mice in the debris and 104 occurrences of this species in the droppings, was interpreted as possible evidence of preference for meadow mice. In this study the ratio of meadow mice to white-footed mice in the diet of the fox was certainly in direct opposition to the relative numbers of these animals taken in traps which possibly is evidence of preference, too. Positive evidence of the capture of 11 meadow mice and 9 white-footed mice by red foxes was found during the study. Of these only one meadow mouse was known to have been left uneaten and unretrieved by foxes, whereas 7 of the white-footed mice were never utilized by foxes.

The complex differential in the interrelationships of the red fox to the meadow mouse and to the white-footed mouse may be explained only after exhaustive research. Contributing to the problem is the difficulty of segregating the species of each form in the fecal material. At least one of the white-footed mice (*Peromyscus maniculatus bairdi*) occupies habitat similar in life form to that of the more common meadow mouse (*Microtus ochrogaster*) on the area. In respect to habitat then these two forms appear to be about equally vulnerable. In addition, trapping records showed that this white-footed mouse was generally more numerous than the prairie meadow mouse.

An appreciable difference exists in the rhythmic behavior of white-footed mice and meadow mice. Johnson (1926) demonstrated that *Peromyscus maniculatus* is normally nocturnal. Hamilton (1937) found *Microtus pennsylvanicus* to be active at all hours. Hatfield (1940) experimentally demonstrated a 2- to 4-hour rhythm of activity at temperatures of from 0° C. to 28° C. for *Microtus pennsylvanicus pennsylvanicus*. At 30° C. and above they were active nearly all the time, and at 0° C. the rhythm was maintained but the length of each term of activity was shortened. Perhaps, also, the rhythm of activity is modified somewhat by cover conditions, for the data of Hatfield (1938) indicated that in sparse cover more meadow mice were taken in traps at night than in day whereas the reverse seemed true in dense cover. In the same experiments *Peromyscus maniculatus bairdi* showed a 24-hour, nocturnal-diurnal rhythm or cycle; they were more active by night than by day. Cold decreased activity and heat produced greater activity but the typical 24-hour cycle was not changed. This marked difference in the rhythmic behavior of the mice together with preference may be of primary importance in bringing about the difference in the relative proportions of white-footed mice and meadow mice in the diet of the red fox.

House Mouse. House mouse (*Mus musculus*) representation was infrequent in the fecal material. In Period I it did not occur, in Period II it appeared 7 times of which 5 were for winter and early spring, and in Period III it was identified only once. It did not appear in 234 droppings gathered at dens.

Murie (1936) found it in only two droppings and other writers did not report it at all.

Muskrat. Paneast (1937) and Smith (1938) indicated that red fox depredations on muskrats in marshes were occasionally severe. There were 45 occurrences of muskrat in the 768 red fox droppings examined on the George Reserve (Murie 1936). Murie indicated that a lack of adequate water in the marsh was largely responsible for the vulnerability of these muskrats.

Errington (1939, p. 185) found that "A large proportion of the muskrats resident in drying out habitats tend to stay in familiar home ranges, and, while they may suffer heavy or even annihilative mortality, they are usually more fortunate than the animals that attempt to go elsewhere." In Iowa the drying up of the water in Big Wall Lake during the summer of 1940 exposed the resident muskrats to the attacks of neighboring foxes (Errington & Scott unpublished). In 79 droppings collected there between June 15 and September 1, muskrat was identified in 70. Late in August heavy rains restored water in the marsh and muskrat abruptly ceased to occur in the fecal passages. Muskrats on the Moingona area almost are confined to the Des Moines River. Although the water in the river was occasionally very low during the summer months the deeper pools were never dry. In this case the foxes would seem dependent upon catching muskrats wandering out on land. That this was unprofitable is evident in the detection of remains in only 2 (Table E, appendix) of the 1,454 fecal passages examined. Muskrat was either absent or infrequent in the material investigated by Hamilton (1935), Dearborn (1932), Errington (1935, 1937), Hatfield (1939) and Nelson (1933). The data show that muskrats living in suitable habitat are not subject to severe red fox predation.

Norway Rat. Norway rat (*Rattus norvegicus*) appeared 11 times in the 1,220 fecal passages collected away from dens, 2 or 0.2 percent of the total occurrences in Period I, 4 or 0.2 percent of the total occurrences in Period II and 5 or 0.3 percent of the total occurrences in Period III. It also occurred in 2 of the 70 fecal passages picked up at dens No. 2 and 3 of the Cyclone Creek family for April 9-11 to 28-30.

Errington (1937) listed it once among 1,010 food items at dens in 1933 and 9 times in 2,848 items in 1934; it occurred 4 times in 1,175 fecal samples from the same dens in 1933 and 5 times in 935 samples in 1934. Hamilton (1935) reported it once in 272 red fox stomachs from New York and New England. In Great Britain Southern & Watson (1941) detected Norway rat in 1 of 40 *Vulpes vulpes* stomachs.

Cottontail. The principal staple food of the red foxes on the Moingona Fox Range was cottontail. It occurred in 920 of the 1,454 fecal passages examined (Tables B, C, E, appendix), and it was the most frequent food found along the trails (Table A, appendix), and around the dens. The findings of

Errington (1935, 1937), Hamilton (1935), Murie (1936) and others show that where cottontails are present they generally make up a substantial portion of the diet. In Great Britain Southern & Watson (1941) identified rabbit (*Oryctolagus cuniculus*) in 17 of 40 stomachs and in 15 of 18 fecal droppings of fox (*Vulpes vulpes*) collected in spring and summer.

The feeding trend on cottontail (Fig. 29) graph-

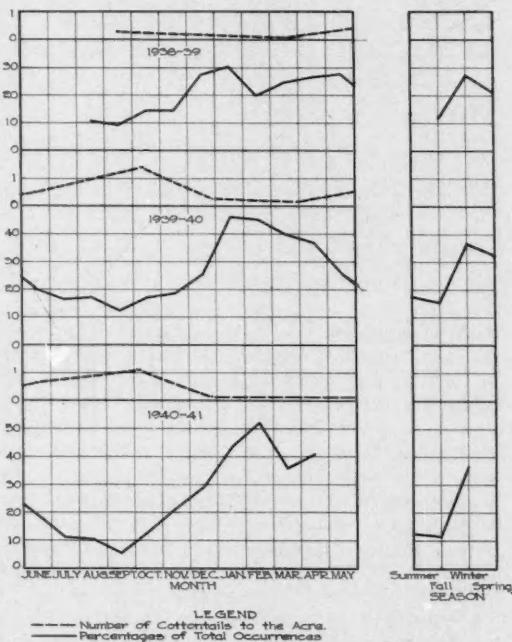


FIG. 29. Monthly trend of cottontail representations in the fecal passages contrasted with seasonal changes in the levels of the cottontail population.

ically demonstrated that appreciably more cottontails are taken in the winter and spring months than in summer and fall. The proportion of cottontail shows a general tendency to pass from a winter high gradually downward to a fall low. The data reported by Murie (1936) also reflect a dietary trend on cottontail similar in direction to those found for similar periods in this study. The shifting of the low in the feeding trend on cottontails from summer as it is in mammals generally and mice specifically to a low in fall presents a striking variation. This is particularly well illustrated in the seasonal trends (Fig. 29).

This marked difference in the cottontail trend as compared with mammals in general may be the result of a high availability and possibly preference for immature cottontails in late spring and summer. The detected occurrences of immature and young cottontails are recorded in Table 5 together with total occurrences of cottontail for analytical purposes. In each year of study immature cottontails first appeared in the food of the foxes in April, were most frequent

TABLE 5. Detected occurrences of immature and young cottontails contrasted with total occurrences of cottontail in fecal material from the trails.

	June	July	August	September	October	November	December	January	February	March	April	May
Period I												
Total occurrences	2	3	11	8	5	6	16	20	6	27	14	10
Immature	1	—	—	—	—	—	—	—	—	—	1	3
Young	2	4	3	2	1	1	—	—	—	—	—	—
Period II												
Total occurrences	13	15	42	26	32	14	26	41	16	27	47	48
Immature	5	6	6	1	—	—	—	—	—	—	51	10 <sup>1</sup>
Young	3	2	10	6	6	2	—	—	—	—	—	5
Period III												
Total occurrences	27	42	13	10	22	24	30	20	19	26	14	—
Immature	10 <sup>1</sup>	11	2	—	5	4	—	1	—	—	2	—
Young	2	3	2	—	5	4	—	—	—	—	—	—

<sup>1</sup>Immature cottontail remains were also detected in fecal passages collected at dens during these months. Of 94 occurrences of cottontail in April, 18 were determined as of immature; of 82 in May, 38 were immature; and of 11 in June, 5 were immature.

in May, June and July and terminated their trend in August and September. This agreed directly with the time and intensity of cottontail nesting in the field. The earliest nest of cottontails found on the area was one in which the young were about five days old on April 15, 1940. Some cottontails were born at an earlier date than indicated by the young in this nest, for on April 21, 1941, a cottontail estimated to be four weeks old was found dead on Second Run. The height of the nesting season occurred in May, June and July. Most of the immature cottontails detected in the fecal material seemed to compare well in size with animals just large enough to leave the nest, indicating that the animals might have been particularly vulnerable at that time. The relative number of immature cottontails taken by foxes may be appreciated only when the tendency for occurrences to vary in direct proportion with the size of prey is considered. The differences noted in the frequency of immature cottontails in the fecal passages from the trails and from the dens have been treated in the section on the influence of age on the feeding trends. Those cottontails classified as young were difficult to determine when they approached sub-adult sizes. The results obtained, however, show that the occurrences of this age class lagged somewhat behind that of the immature group both in time and frequency, the latter despite of their larger size. This would indicate that the immature animals were comparatively more vulnerable than the young or that fewer animals reached the young classification because of high mortality in the immature group. In their study of the spring and summer food of the fox (*Vulpes vulpes*) in Great Britain Southern & Watson (1941) found young rabbits (*Oryctolagus cuniculus*) in 6 of 40 stomachs.

An inventory of cottontails was taken on the quadrats at regular intervals in order to provide some

basis for determining the relationship of population levels to dietary proportion. Differences in the cottontail population levels are somewhat accentuated by response of the cottontails to the seasons. The movement of cottontails in and out of wintering quarters and cultivated fields tends to make somewhat more marked changes than actually existed. The population levels are averaged from the counts obtained on all the quadrats and are therefore representative of the area as a whole instead of any one particular cover type.

It is manifest that the annual fluctuation of the population has little to do with the direction taken by the annual feeding trend (Fig. 29). From comparisons of season data it is clear that the proportion of cottontail in the diet shows a tendency to respond to year to year changes in population levels for the same time of year (Table 6).

TABLE 6. Comparison of the average number of cottontails to the acre on the quadrats with the percentages of total occurrences for cottontail in the fecal material.

	Cottontails to the acre	Percentage of total occurrences
<b>FALL</b>		
September, 1938	0.25	9.4
October, 1939	1.40	17.2
October, 1940	1.10	13.3
<b>WINTER</b>		
December, 1938	0.20	27.7
December, 1939	0.29	25.6
December, 1940	0.14	29.0
<b>SPRING</b>		
March, 1939	0.10	24.8
March, 1940	0.17	39.6
March, 1941	no count made	35.8
<b>SUMMER</b>		
June, 1939	0.50	20.1
June, 1940	0.65	19.1

Jack Rabbit. This rabbit was never known to occur within the area except in winter when an occasional one appeared on the cleared upland. It was identified once in a fecal passage collected in February, 1941. Many of the localities investigated by Errington (1937) were well within jack rabbit ranges and jack rabbit was recorded 201 times among 3,858 food items about dens and it occurred 63 times in 2,110 fecal samples collected about the same dens.

#### HOOVED MAMMALS

Domestic Pig. Domestic pig (*Sus scrofa*) occurred 10 times in the 1,220 fecal passages gathered away from dens and 6 times in the 234 passages picked up on the den sites. No live pigs were reported by farmers to have been lost to any predator and all occurrences of pig in the fecal material could be associated with dead animals discarded by local farmers. Once when 7 little pigs killed by the sow were thrown out a farm dog was known to have competed with the foxes in feeding on them. The formidably tusked boar's head that appeared at the fox den on Bear Creek on June 23, 1939, certainly did not indi-

eate fox predation on hogs. One marvels at the ability of the fox to drag or carry this heavy head from where it had been discarded at a local farmstead.

**White-tailed Deer.** Remains of an adult deer were found in one of the passages of February, 1941. Murie (1936) found remains of 3 adult deer in the 768 droppings that he examined on the George Reserve, but no evidence that foxes had harmed fawns dropped there late in May and June was obtained.

#### BIRDS

Technical limitations make specific determinations of bird remains in fecal passages very difficult. Evidence of this is the large number, 191, of the 470 bird occurrences that could be classified only as undetermined avian remains (Tables B, C, F, appendix).

Ten of the undetermined bird occurrences were fragments of egg shells. These were the only records of egg remains in the fecal material except for three of domestic chicken and three of ring-necked pheasant. Five of the egg shell appearances listed as undetermined were qualified as probably domestic chicken and were taken in September and October, leaving only eight occurrences, five undetermined and three of ring-necked pheasant that were detected during the nesting season. Probably all of the ring-necked pheasant egg shell fragments were from one nest, for all were found in the fecal samples from the same den in May, 1940. Some of the egg shells may have been obtained as a secondary food when female birds were eaten just prior to egg laying. This would have been possible in the case of one carrion hen located where it had been discarded in the field. No bird nest was known to have been destroyed or disturbed by foxes.

In the fecal material 279 of the bird determinations could at least be designated as nongame or game. The percentages of the total number of occurrences for these two categories in droppings from the trails were: Period I, nongame 12.1, game 1.8; Period II, nongame 8.2, game 1.1; and Period III, nongame 4.4, game 1.2 (Table F, appendix). The ratio of game determinations to nongame determinations in the droppings collected at the dens (Tables B, C, appendix) were roughly the same as those for the trails.

#### NONGAME BIRDS

**Domestic Poultry.** Domestic chicken proved to be the principal avian food identified in the fecal material. In the trail feces it made up 7.4 percent of the total occurrences in Period I, 3.1 percent in Period II, and 2.1 percent in Period III (Table F, appendix). It was detected but twice in the 234 scats collected on the den sites. It is generally agreed that a large part of the domestic chicken fed upon by foxes is carrion (Errington 1935, Hamilton 1935). Nearly all of the occurrences of domestic chicken in the fecal material from the Moingona area could be associated with available carrion. A small but al-

most continuous supply of carrion chicken reached the fields within the ranges of the foxes. On one occasion a large number of dead chickens were thrown out at the edge of River Road in the southeast part of the area, but this supply could not be associated with chicken remains in droppings collected at the time. These chickens were outside the interpolated home range of the resident foxes, and possibly for this reason they were not found, and if found, then only after the material had advanced to such a state of decay as to have been unattractive as food.

As in the experience of Errington (1935), red fox predation was the source of severe losses to a vulnerably situated flock of domestic poultry. In August, 1938, substantial 17.6 percent of the total food occurrence was found to be domestic chicken. This resulted from depredations on a flock that had been temporarily forgotten during a domestic emergency at a local farmstead. The exact number of the original flock had not been recorded, but it was estimated to have been about 50, of which the foxes took nearly one-fourth.

In November, 1940, remains of guinea fowl were detected three times, the only occurrences listed. These remains could, almost with certainty, be associated with a dead bird discarded at a local farmstead.

Several of the resident farm families were direct descendants of original settlers in these hills along the Des Moines River. These people, as a matter of course, followed the practice of keeping their poultry penned at least from early evening to the following mid-morning. This seemed to have become a somewhat time-honored method of avoiding losses from the numerous predators associated with the "river land."

**Owls.** In October, 1939, a barred owl was shot by hunters and left on upper Polly Creek. Tracks showed that foxes passed within inches of this bird many times, and once a fecal dropping was collected beside the carcass. Although certainly aware of its existence the foxes did not eat any of the carcass even though it remained in a fair state of preservation for some time. Possibly, the foxes first located the bird while it was still heavily associated with scent from human handling.

Remains of owls were twice detected in scats from the trails and three times in those from the den sites. Feather characteristics marked one of the occurrences as either *Asio* or *Bubo*. The three determinations of owl remains in the fecal samples from the dens were collected at the same time that a barred owl was listed among the food litter there. Errington (1935) reported a juvenile great horned owl and a long-eared owl (*Asio wilsonianus*) among 1,010 food items found at red fox dens in 1933.

**Woodpeckers.** The hairy woodpecker was represented in one of the trail droppings, the only positive identification of woodpecker remains. In 11 of the fecal passages the diagnostic parts were definitely

determined as being either of woodpecker or perching bird.

Perching Birds. The proportion of perching birds (Passeriformes) identifications to total occurrences in droppings from the trails was 3.8 percent in Period I, 3.7 percent in Period II, and 2.0 percent in Period III (Table F, appendix). Because of technical difficulties from one-fourth to one-half of the perching bird representations had to be listed as undetermined. About the same proportion of the 33 perching bird representations in the 234 passages picked up at the dens was recorded as undetermined (Tables B, C, appendix). Of the determined perching bird remains most were of such infrequent occurrence in the fecal material that they seemed to have been taken more by chance than because of any particular species vulnerability. Among these were the blue jay, black-eared chickadee, robin (*Turdus migratorius*), meadowlark (*Sturnella* sp.), English sparrow (*Passer domesticus*), cardinal and goldfinch (*Spinus tristis*). At the dens a blue jay, a robin, a starling (*Sturnus vulgaris*), and the feathers of several passerine birds were noted. On January 18, 1939, a red fox dug a crow wing out of the snow but discarded it without eating any of it. A swamp sparrow (*Melospiza georgiana*), a white-breasted nuthatch and remains of a nighthawk (*Chordeiles minor*) were found where they had been left by foxes. Of perching birds that were represented importantly at times in the fecal material were fringillids apparently killed or weakened during blizzards and periods of extreme cold. The species principally affected, as identified in the fields and in the passages, were slate-colored juncos (*Junco hiemalis*) and tree sparrows (*Spizella arborea*). These were particularly evident following general emergency conditions in February, 1939, and January, 1940, and after the severe unseasonal blizzard of November 11, 1940 (Scott & Baskett 1941).

Bob-white. Bob-white remains were identified in only 7 of the 1,454 fecal passages examined. Even considering the difficulty of identifying specific avian remains, these records fail to reflect severe fox pressure on bob-whites on the Moingona area. Bob-white was represented only once in 79 red fox stomachs, intestines and complete fecal passages collected in Iowa in winter (Errington 1937). In Minnesota on the northern edge of bob-white range Hatfield (1939) did not detect its remains in 29 winter stomachs. Quail remains were detected once in 15 red fox stomachs collected in January and February in Virginia (Nelson 1933).

The extensive research of Errington & Hamerstrom (1936) demonstrated that predation losses to quail in winter were exacted particularly from populations in excess of carrying capacity. Carrying capacity determinations were not made for the covey territories on the Moingona area. During winter, 1938-39, there were nearly 125 bob-whites, or 1 to 16 acres, on the area; in winter 1939-40, a minimum of about 200, or 1 bird to 10 acres, was estimated, and the

best winter (1940-41) count showed only 49 birds, or an average of about 1 to 40 acres. The occurrences of bob-white remains in the fecal material are obviously too few to lend much significance to analysis. However, during Period I, but a single determination of bob-white was recorded and that was in March. In Period II there were six identifications, two of which occurred in winter and four in spring. On January 20, 1940, sheared-off quail feathers were found together with tracks, indicating that the foxes had fed on two of these birds. Fair evidence indicated that these birds had died as a result of deep snow and severe cold. During Period III, when the bob-white population was at its lowest, remains of quail were not found in the fecal material.

Ring-necked Pheasant. The ring-necked pheasant was never present in large numbers. There were a few more birds on the area each winter than at any other time as a result of movement into winter concentrations. In winter an average of about 1 bird to 30 acres was considered a reasonable estimate of the population over that part of the area north of Bear Creek, and there was a slight winter to winter increase.

Although a few more identifications were made for pheasants than for bob-white (Table F, appendix), there were still too few to reveal much of the pheasant-fox relationship. Of the total occurrences in Period I, pheasant determinations made up 1.4 percent, in Period II 0.6 percent and in Period III 1.0 percent. Among the 222 droppings collected at rearing dens in 1940, 5 pheasant occurrences, of which 2 were egg shell fragments, were listed (Table C, appendix). Pheasant was located in five places where it had been fed upon by foxes in the field, and was listed once among the food debris at the den sites.

A comparison of the seasonal frequency of pheasant remains in the fecal material collected on trails indicates a tendency toward greatest relative proportion in winter and spring. It is possible that the winter increase in occurrences may be associated with severe weather and the gregarious tendencies of the birds, and in spring with the excitement of courtship and the onset of nesting.

In 79 stomachs, intestines and complete fecal passages collected in Iowa in winter ring-necked pheasant remains were detected 5 times, while in spring and early summer pheasant was represented 173 times in 2,110 fecal passages collected about dens (Errington 1937). Hatfield (1939) found that pheasants made up 4.0 percent of the bulk in 29 red fox stomachs collected in winter and early spring in Minnesota.

Mourning Dove. Mourning doves were scarce on the area throughout most of the year. They were present in appreciable numbers only in the fall when flocks stopped to feed in hemp patches. These flocks of doves usually first became obvious in the hemp about mid-September and were largely gone by November. It is perhaps of significance then

that four of the five mourning dove identifications occurred in the fall. By month their occurrences were: August, one; September, one; October, two; and November, one.

#### COLD-BLOODED VERTEBRATES

The remains of a blue racer (*Coluber constrictor*) were detected in 1 of the 1,454 fecal droppings examined. This constituted the only determination of cold-blooded vertebrate in the material studied.

In the field, of a toad (*Bufo americanus*) found where it had been left on the trail, nothing remained but the hind legs and the skin of the back. Possibly the poison glands of the back proved distasteful.

Lower vertebrates were represented in 24 of the 2,110 fecal passages collected in spring and early summer at dens of red foxes (Errington 1937).

#### INVERTEBRATES

Gastropods and Diplopods. Undetermined gastropods were detected three times in the fecal passages. Diplopods appeared four times; in two, *Polydesmus* and *Julus* were identified, while two were undetermined. The remaining invertebrate occurrences were insects.

Insects. Fecal analyses showed that insects made up a very substantial proportion of the warm weather diet of the foxes (Tables B, C, G, appendix). In this the data of Hamilton (1935), Errington (1937), Dearborn (1932), Murie (1936) and Hamilton, Hosley & MacGregor (1937) agree. The findings of Southern & Watson (1941) and of Baranovskaya & Kolosov (1935) have been interpreted as showing that insects do not form a very large part of the diet of *Vulpes vulpes*.

Nearly all of the insects taken were in the adult form in the orders Orthoptera and Coleoptera. While over 50 kinds of insects were identified, the bulk of the insects in the diet was made up of: *Melanoplus* spp., *Amblycorypha oblongifolia*, *Gryllus assimilis*, *Calosoma* spp., *Geotrupes*, *Phyllophaga* spp. and *Lucanus* sp. The trends of these insects are presented in graphs (Fig. 31).

Orthoptera. *Melanoplus* grasshoppers were probably taken in greater relative amounts than any other insect. They first appeared in the seats in June or July, reached a peak in fall and continued appearing to a limited extent as late as January (Fig. 30). Those that were detected in the winter months and some that regularly occurred in March were thought to have been adults preserved by the cold. Experience with feeding caged foxes indicated that grasshoppers are relished. Most of these grasshoppers were identified as *Melanoplus differentialis* and red-legged forms such as *M. femur-rubrum*. Other Acrididae, occurring in from 1 to 13 of the passages were: *Orphulella pelidna*, *Arphia*, *Chortophaga* sp., *Hippiscus rugosus*, *Pardalophora* sp., *Dissosteira carolina*, *Schistocerca*, and *Trachyrachis kiowa*.

*Tettigoniidae* would have been represented in relatively few samples if it had not been for the large number of *Amblycorypha oblongifolia* taken during the summer of 1939 (Fig. 30), of which no trace was detected at any other time. As eggs were associated with remains of the adults of this species in 31 of its 54 occurrences, the insects were probably taken during oviposition. Seventeen occurrences of *Tettigoniidae* were undetermined and *Microcentrum* sp., *Conocephalus* sp. and *Ceuthophilus* sp. were each identified once.

*Gryllus assimilis*, the only representative of the Gryllidae in the seats, was among the first live spring insects taken by the foxes (Fig. 30). It appeared 95 times in the droppings collected on the trails, 12 times in 73 seats picked up in May at dens of the Cyclone Creek family, in 4 of 16 fecal samples collected in June at den sites of the Second Run family, and in 1 of the 12 droppings from dens in May, 1939.

Odontata, Homoptera and Hemiptera. An undetermined dragon-fly occurred once. Homoptera was represented by two identifications of Cicadidae. In four appearances of Hemiptera five species were identified as follows: *Euschistus variolarius*, *Cicosternum hilare*, *Acrosternum* sp., *Piesma cinerea* and *Blissus leucopterus*. The latter two, the piesmid and the chinch bug, were almost certainly taken by accident.

Lepidoptera and Diptera. Lepidoptera were de-

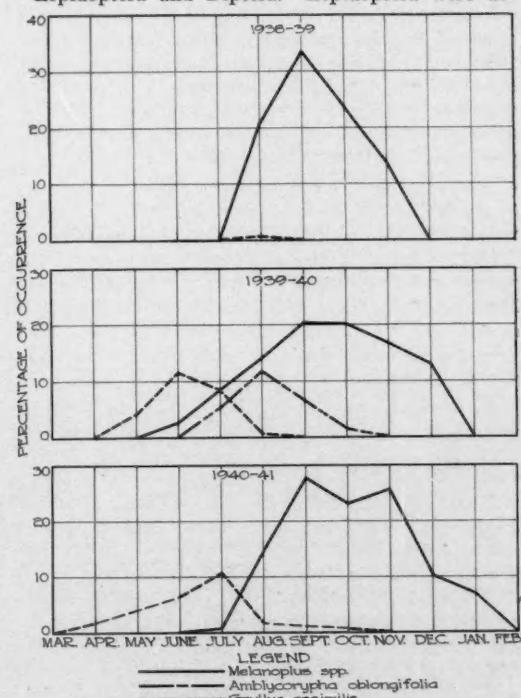


FIG. 30. Monthly trends of the principal Orthoptera in the diet.

teeted in 7 of the 12 seats from the den in May, 1939, in 12 of 222 droppings picked up at dens in 1940 and in 19 of 1,220 collected on the trails. All were larvae except two from the trail material. Geometridae occurred once and among the Phalaenidae were 11 *Nephelodes emmedonia* and 2 *Paipaipema* sp. Seven appearances of *Nephelodes emmedonia* and 1 of *Paipaipema* sp. were for the 12 passages collected at the den in May, 1939.

Diptera appeared 4 times in 222 passages collected at dens in 1940 and 21 times in the trail passages. Fourteen of the fly occurrences were for asilids and one was for larval sarcophagids that had no doubt been taken with carrion.

Coleoptera. More species of Coleoptera were identified than for any other order. Eleven of its families were represented.

*Cincindela sexguttata* was identified once to represent the Cincindelidae.

Carabidae was recorded 201 times in the 1,220 passages collected on trails, and 69 times in 234 from the dens. The many forms in this family make specific determinations difficult, and as a result 96 or about half of occurrences in the trail material and 33 or about half of the occurrences in den seats could not be determined. *Calosoma* spp. were common in the passages (Fig. 31), occurring 74 times in the trail passages and 52 times in 234 passages from den sites. Of these *Calosoma calidum* was the most common while *C. scrutator* and *C. externum* appeared to a lesser extent. Other determined Carabidae and the number of times each occurred were: *Carabus* spp. 6, *Elaphrus ruscarius* 1, *Pasimachus elongatus* 7, *Dicaelus sculptilis* 2, *Scarites* 7, *Evarthrus* 34, *Chlaenius* 13, *Harpalus caliginosus* 46, *H. pennsylvanicus* 1 and *H. pleuriticus* 1.

Hydrophilidae was represented once by *Hydrous triangularis*. Necrophorus was identified four times in five detections of Silphidae. Undetermined Staphylinidae occurred three times and Tenebrionidae appeared once. Of the five records for Elateridae *Monocrepidius auritus* was identified twice and *Melanotus* sp. once. For Nitidulidae, *Glischrochilus fasciatus* occurred once. Undetermined Erotylidae was detected once.

Scarabaeidae were recorded 234 times in the trail droppings and 87 times in the 234 fecal samples from the den sites. The members of this family were more easily identified than those of Carabidae, and only 11 were listed as undetermined. *Canthon laevis*, *Trox* sp., *Ataenius ovatus* and *Ligyrus relictus* each occurred once. There were a few appearances each for *Copris anaglypticus*, *Onthophagus*, *Aphodius*, *Bolboceras*, *Pelidnota punctata*, *Xyloryctes satyrus* and *Euphoria*. Represented more importantly was *Bolbocerasoma farctum* with 35 occurrences, *Ligyrus* with 22, *Geotrupes* with 73 and *Phyllophaga* spp. with 205. The trend of *Geotrupes* and *Phyllophaga* spp. representations in the fecal material is shown in the graph (Fig. 31). Occurrences of *Geo-*

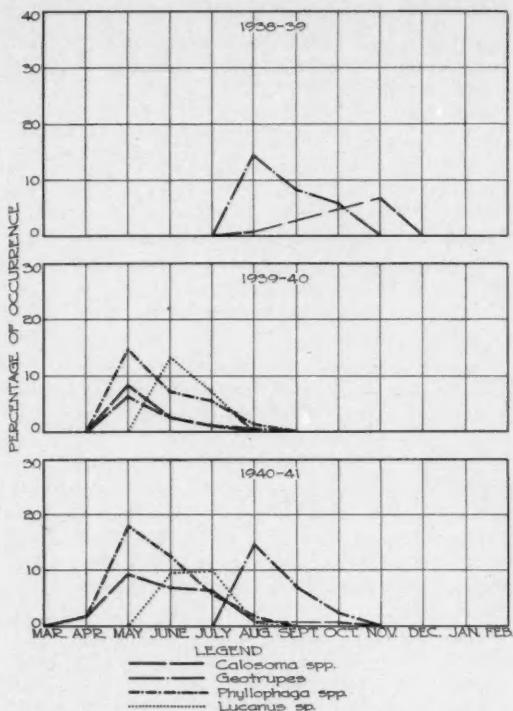


Fig. 31. Monthly trends of the principal Coleoptera in the diet.

*trupes* were relatively fewer and ceased earlier in 1939 than in 1938 and 1940.

*Lucanidae* occurred 92 times in the 1,454 passages. All were for *Lucanus* sp., probably *dama*, except for one occurrence of *Dorcus* sp. *Lucanus* sp. was recorded only once in Period I, probably because of the few passages collected in June and July when it ordinarily appeared. In Period II and III it occurred 22 and 69 times, respectively, with a trend as in the graph (Fig. 31).

*Chrysomelidae* was represented in two droppings, once by *Typhophorus canellus*. *Circulionidae* was listed by reason of one appearance of *Anametis granulatus*.

*Hymenoptera*. *Hymenoptera* occurred 89 times. Of these, 2 were *Andrenidae* and the remainder were *Formicidae*. As the *Formicidae* were usually represented by one and never more than a few adult individuals it was considered very probably that they were taken incidental to feeding on other foods. It seems likely that if these insects had been taken from a hill greater numbers of individuals as well as larvae and pupae would have been found. The forms identified and the number of occurrences of each were: *Formica* 3, *Myrmica brevinodis* 22, *Ponera* sp. 1, *Aphaenogaster* 8, *Prenolepis imparis* 19, *Lasius* sp. 1, *Tapinoma sessile* 5, *Solenopsis* 5, and *Camponotus pennsylvanicus* 5. The remainder were undetermined.

## PLANTS

Grass-Sedge. Blade-like leaves, typical grasses and sedges, were found in 62 of the seats from the trails and in 3 of the fecal samples collected at the dens. The data show a tendency towards greater frequencies of grass-sedge-like leaves during the cold weather months (Table H, appendix). Much green "grass" was found in 1 of 40 red fox stomachs taken between December 17, 1932, and June 13, 1933, in Iowa (Errington 1935). Hamilton (1935) found that "grasses" made up 13.9 percent of the total food in 206 red fox stomachs collected during the fall and winter in New York and New England. "Grass" made up 2.6 percent of the total food bulk in 29 red fox stomachs collected in winter in Minnesota and made up practically the entire contents of 2 stomachs (Hatfield 1939). In this study six droppings were collected that were composed entirely of grass-sedge-like leaves, identified as Carex in one seat. The contents of two fecal passages were largely Carex with some grass. The contents of another were about 75 percent grass and about 25 percent Carex. Grass alone was found in two, probably Muhlenbergia, in one case and Poa in the other. In Russia, Baranovskia & Kolosov (1935) found a fecal passage of *Vulpes vulpes* that was composed entirely of Carex leaves.

Corn. Fragments of corn kernels occurred 54 times in the fecal material examined. Corn was often accompanied by silk, indicating that it had been chewed directly from the cob. Corn kernels that were not crushed and could be associated with avian remains were not included as food. Most of the fall occurrences were of corn in the "milk stage." As with the grass-sedge leaves there is a tendency for the corn to be most frequent during the cold weather months (Table H, appendix). This is quite likely a kind of compensatory trend resulting from the usual high availability of fleshy fruits in the warm weather months. Corn made up a greater part of the total occurrences in Period I (3.8%) when the crop of fleshy fruits was very light than in Period II (1.6%) and Period III (1.3%) when fleshy fruit was abundantly available. Corn was recorded five times in the winter, spring and early summer material reported by Murie (1936).

Oats. Oat grains were detected in four of the fecal passages, one in December, 1939, and three in December, 1940. These occurred in some quantity and were not associated with bird remains. In two of the representations hulls were present, indicating that the grain may have been pulled from shocks left in the field.

Acorns. Murie (1936) listed acorn from 2 of the 768 fecal passages collected in winter, spring and early summer on the George Reserve. On December 29, 1939, following light snow, a fox in the Miongona area had worked around beneath some oak trees scratching out acorns, of which freshly broken fragments indicated that the acorns had been chewed. During Period I acorn remains appeared twice

(0.4%), once in January and once in March. In Period II they occurred 48 times (3.1%), 40 of which were detected in passages for September and October. In Period III there was but a single occurrence (0.1%). This mast crop in the fall of 1939 was heavy, but it did not seem to be as proportionately greater than in 1938 and 1940 as its occurrences in the passages indicated.

Elm Seeds. There was an extremely heavy yield of elm seeds on the area in May and June, 1940, and elm seeds occurred in substantial amounts in 10 of the 47 fecal passages collected on the trails in June. They appeared in 8 of 89 passages for May and in 4 of 16 passages for June collected at the den sites. The seeds did not seem to have been affected by the digestive processes.

Mulberry. In 1938 the remains of mulberry fruits were not found in the droppings, possibly because of a light crop, few summer fecal samples (36), and the lack of agreement in the location of the territories of the foxes and the location of the trees. In 1939 none was recorded, probably because the territories of the foxes did not include the three locations. In 1940 when the territory of at least one family of foxes included most of the tree locations mulberry was detected 110 times as follows: June 4 (3.0%), July 96 (24.3%), August 7 (4.2%) and September 3 (1.6%). These trends are shown in the graph (Fig. 32) for comparison with those of the other fruits.

Gooseberries. Remains of gooseberry fruits were not detected in 1938. In 1939 they occurred 33 times

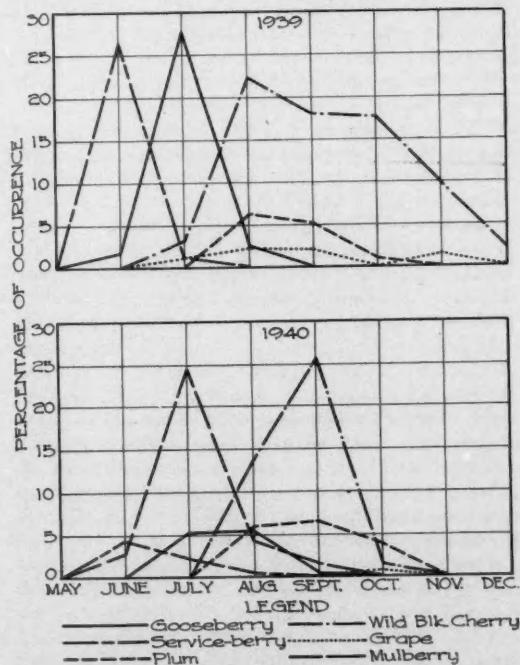


FIG. 32. Monthly trends of fleshy fruit representations.

as follows: June 1 (1.7%), July 24 (26.5%) and August 8 (2.7%). In 1940 there were 31 appearances as follows: July 21 (5.3%), August 9 (5.4%) and September 1 (0.5%) (Fig. 32).

Apple. Apples have been reported among the winter foods of red foxes (Hamilton 1935). Cultivated apples were not known to have been available to the foxes on the Moingona area, and the remains of these fruits were not detected in the fecal material. Fruits of the red haw and western crab apple were present and easily available to the foxes. Only one occurrence (western crab apple), however, was detected in the droppings inspected.

Rose. The seeds and skins of rose hips were detected in one dropping.

Service-berry. The remains of the fruit of the service-berry were detected 33 times in the 1939 and 1940 seasons, mainly in June. The trend is shown in the graph (Fig. 32). In 300 fecal passages collected in 1930, Dearborn (1932) found 31.5 percent of the volume to be plant remains, of which remains of service-berry made up 64.8 percent.

Plum. Fruit remains of the American plum were detected in 64 of the fecal passages examined. None occurred in 1938, but in 1939 there were 36 appearances as follows: August 19 (6.4%), September 15 (5.2%) and October 2 (1.0%). In 1940 it was detected 28 times as follows: August 10 (6.0%), September 13 (6.8%) and October 5 (4.0%).

Cherry. Hamilton, Hosley & MacGregor (1937) found wild black cherry (*Prunus serotina* = *Padus virginiana*) 71 times in 131 mid-summer seats from Massachusetts, the most frequent food listed. In this study the fruits of wild black cherry did not occur during the first year, but in 1939, they occurred 165 times as follows: July 3 (3.4%), August 67 (22.6%), September 52 (18.2%), October 35 (17.8%), November 6 (9.8%) and December 2 (2.1%), and 74 times in 1940 as follows: August 23 (13.8%), September 49 (25.6%) and October 2 (1.6%).

Grape. A few occurrences of grape were noted by Murie (1936) and Hamilton, Hosley & MacGregor (1937). In the material from the Moingona area they did not occur in Period I, and in Period III when the grapes did not fruit abundantly there was only one representation. In Period II the remains of the fruit of the grape were identified 15 times as follows: July 1 (1.1%), August 7 (2.4%), September 6 (2.1%) and November 1 (1.6%).

Catmint. The seeds and seed heads of catmint (*Nepeta*, prob. *Cataria*) appeared three times in the fecal material examined. Once a seed head of this plant was found along a fox trail in the snow where it had apparently been dropped.

Ground-cherry. The seeds and skins of the ground-cherry (*Physalis*) were identified in 11 of the fecal passages examined.

Black Nightshade. The seeds and skins of the fruit of the black nightshade (*Solanum nigrum*) appeared in eight droppings.

Horse-nettle. The seeds and skins of the horse-nettle (*Solanum carolinense*) were found in three seats.

#### NON-FOODS AND ITEMS OF QUESTIONABLE DIETARY VALUE

Dirt, sand and gravel were recorded, usually in insignificant amounts. On two occasions over one-half of the passage contents was loam, indicating that this material had probably not been accidentally taken. Sand and gravel appeared with considerable regularity in seats containing mulberries during July, 1940, when there was much fox activity about a mulberry tree, the fruit of which fell on the sand and gravel of a dry run. Several times small amounts of gravel were thought to have been the grit content of avian prey. A folder of safety matches and piece of tire tube were recorded. Single lead shot, about No. 6 size, appeared in two seats, one accompanied by cottontail remains, and the other by cottontail and pheasant.

Miscellaneous plant material was frequently in the passages: pieces of rotted wood, bits of grass or sedge, sections of twigs, old weed stems, rootlets, fragments of moss, and once hazelnut eatkin. Occasionally, unbroken seeds or chewed plant material seemed to be crop or stomach contents of prey, the importance of which for the foxes is difficult of evaluation.

Some plant debris may enter the digestive system in play. On three separate occasions the nut of the butternut (*Juglans cinerea*) was observed to have attracted the attention of foxes. Twice the nut seemed to have served as an object for play, probably by young foxes. Another time the nut was found where it had been dropped in the snow along a fox trail in mid-winter. The trail had been followed for approximately one mile, and it was not considered likely that the fox had obtained the nut in that distance. Possibly these nuts hold some attraction for foxes other than as items of food.

In addition to seeds of fruits taken as food, many evidently were ingested with prey and by accident. A seasonal analysis of the non-food seeds taken from 1,220 passages collected away from rearing dens is presented in Table I, appendix.

In July, 1939, the deciduous molar,  $dm_3$ , of a young fox was extracted from the contents of a fecal passage, indicating that it had been swallowed by a young animal losing its first teeth. Another passage in May, 1940, was found to contain two deciduous incisors of a young fox. Wisps of fox fur were taken from among the food remains in 18 of the 1,220 passages collected away from dens; in 5 of these cases *Lappula echinata* seeds accompanied the fur, indicating that the fur had been swallowed following a carding operation. Of the 18 occurrences 8 were in late summer seats, 5 in fall, and 5 in spring. In the 222 passages examined from about rearing dens in spring, 1940, fur occurred twice.

In the 234 seats collected about rearing dens there was only 1 occurrence of parasitic insect, an immature bird louse (Gonioctenes), accompanied by the remains of the probable host, a ring-necked pheasant. In the 1,220 passages collected away from dens bird lice occurred 4 times, all with avian remains. Two were undetermined, and two, identified as *Ricinus* sp., were associated with the remains of slate-colored juncos.

No fleas were found in the seats collected at the rearing dens, but in the 1,220 passages collected away from the rearing dens 6 species occurred 14 times. *Cediopsylla simplex*, found in six passages, in Iowa has been reported from *Sylvilagus floridanus*, *Vulpes regalis* and *Blarina brevicauda* (Fox 1940). *Cediopsylla simplex* was also collected on the dead young fox previously mentioned. Cottontail remains were present with *Cediopsylla simplex* on all but one occurrence, when it was accompanied by *Mierotus* and *Peromyscus* remains. *Hoplopsyllus affinis*, identified in six passages, in Iowa has been reported on the "house rat," "red fox" and "cottontail" by Fox (1940) and on *Vulpes regalis* by Smith (1943). Cottontail remains were included with each *Hoplopsyllus affinis* representation. *Ctenophthalmus pseudagyrtes* appeared once with remains of cottontail and *Mierotus* both of which have been indicated as hosts (Fox 1940). *Opisocroctis brunneri*, common on *Sciuridae*, was found once, accompanied by cottontail and *Mierotus* remains. There were two occurrences of *Epitedia wenmanni*, once with *Peromyscus* and *Mierotus* remains and once with cottontail remains. It has been reported on *Mierotus* and *Peromyscus* but not on cottontail. *Megabothris wagneri*, found in one passage, was accompanied by remains of *Mierotus* and thirteen-striped ground squirrel.

When the northern white-footed mice on the area were infested with *Cuterebra*, probably *fontinalis* (Scott & Sneed 1942), a larva of this warble was found in a passage defecated October 1 or 2, 1940, together with remains of its probable host.

Analysis of the fecal passages also revealed parasitic arachnids. In August, 1938, a mite, *Machrocheles* was listed twice, each accompanied by *Geotrupes*, a scarabaeid on which the mite is a symbiont. *Ixodes kingi* was collected on the head of a young red fox from Rockwell, Iowa, on April 18, 1938. The cottontail tick, *Haemophysalis leporis-palustris*, was identified 8 times in the 1,220 fecal passages located away from rearing dens. In 1938 there was one occurrence in passages dated for October; in 1939 there were two in June, one in May and three in October; in 1940 one appeared in May. The single individual to an occurrence was accompanied by remains of cottontail. In the 12 passages gathered at a rearing den in May, 1939, this tick occurred once. In the 222 passages from rearing dens in the spring of 1940 there was one occurrence of an immature *Haemophysalis* in April and another was recorded early in May. Late in May an adult

*Haemophysalis leporis-palustris* appeared in one of the passages. All of these were found in the 156 passages collected about the rearing dens of the Cyclone Creek family. None was found in the 66 passages collected at the rearing dens of the Second Run family.

The common dog tick (*Dermacentor variabilis*) appeared regularly in spring and summer passages. Table 7 shows the frequency of occurrences of this

TABLE 7. Monthly occurrences of the common dog tick in passages collected away from rearing dens.

	March	April	May	June	July	August	September	October	November
1938									
Number Passages . . . . .	...	...	...	3	5	28	19	12	17
Number Occurrences . . . . .	...	...	...	...	2	...	1	...	...
1939									
Number Passages . . . . .	50	22	12	25	33	74	60	47	22
Number Occurrences . . . . .	...	3	3	3	4	3	...	1	...
1940									
Number Passages . . . . .	36	60	58	47	127	43	57	39	30
Number Occurrences . . . . .	...	1	6	8	4	2	...	...	...

tick in the passages collected away from rearing dens. Adult and immature forms were not reported for this analysis. In the 12 passages picked up at a rearing den in 1939 there was an occurrence of this tick and another tick that was probably this species. Of the 73 passages collected about the rearing dens of the Cyclone Creek family in May, 1940, there were 14 occurrences, but it did not occur in 83 passages that were collected from the family in April. In the 50 passages collected around the rearing dens of the Second Run family in April and May, 1940, no dog ticks were observed, and one was found in the 16 passages collected from this family early in June. A generally greater frequency of dog ticks in the passages of the Cyclone Creek family than in those of the Second Run family reflects a territorial difference. In May the Second Creek family occupied dens in the closely grazed pasture land with a somewhat open stand of trees and little brushy undergrowth. The Cyclone Creek family occupied dens in brushy second growth. The latter appeared to represent good environment for the dog tick. Three specimens of the dog tick were taken from the young fox found dead at the Range on May 31, 1940.

Nematodes in the fecal passages were *Toxascaris leonina* in two passages and *Toxascaris*, probably *leonina*, in one. Smith (1943) found *Toxascaris leonina* to have a greater frequency of occurrence than any other internal parasite of Iowa foxes, with 140 appearances in 234 carcasses. *Physaloptera*, probably *felidis*, was taken from three passages. Smith (1943) identified *Physaloptera felidis* in 80 of 234 fox carcasses.

## SUMMARY

1. The Northern Plains red fox was studied intensively on the Moingona Fox Range in the Des Moines River Valley in central Iowa, from June, 1938, to June, 1941, with particular attention for the interrelationships resulting from the fox's feeding.

2. The research was accomplished by field and laboratory methods involving some experimentation with captive animals.

3. Observations in the field were most productive when concentrated on the evidences of "signs" left by the red fox in its life's activity.

4. The home range, movements and life history of the red foxes were importantly related to the food interrelationships, because the animals naturally fed within the limits of their living space.

5. The feeding tendencies were investigated by analysis of fecal passages because the number of samples available made possible a continuous determination of the relative proportions of the foods consumed.

6. During the study 1,454 fecal passages were collected and analyzed; 234 of these were picked up at dens.

7. The red foxes were found to be primarily carnivorous, consuming substantial quantities of insect and plant foods when available.

8. Warm-blooded vertebrates were less frequent in the warm weather diet than in the cold weather diet, whereas the reverse was true for insects and plant foods.

9. The principal staple foods were cottontails and mice, especially *Peromyscus* and *Micromyscus*.

10. The red foxes seemed to possess these food preferences: The meadow mouse was high on the scale of preferences, insectivores and weasels were regularly left uneaten, weasels appeared to be particularly unsatisfactory as food, and carrion that was advanced in decay did not seem to be attractive food for the foxes.

11. These differences were noted in a comparison of the frequency of occurrences of the principal food groups in the fecal passages from the trails and those from the dens: In April, when the pups were most dependent upon the adults for food, the remains of warm-blooded vertebrates were more frequent in the fecal material from the dens than in that from the trails, and limited occurrences of invertebrate and plant remains were detected in passages from the trails while neither were found in passages from the dens; in May, when the pups were presumably less dependent on the adults, warm-blooded vertebrates were not so frequent in the den material and were more frequent in that from the trails, while the invertebrate and plant representation markedly increased in the passages found at the dens.

12. Within the limits of its fundamentally carnivorous nature the red fox was mainly influenced in its feeding by availability of foods, and on the whole the proportions of individual food items seemed more to reflect relative than specific availability.

13. Fluctuations in the frequency of occurrences of some foods for which no appreciable change in availability was evident resulted simply because other foods became relatively more or less available.

14. There seemed to be no important lack of utilization of suitable foods as foxes ate carrion not too far advanced in decay and frequently items that they killed and did not eat were readily consumed by animal associates.

15. So far as could be determined foxes did not exert a dominant influence on the populations of the prey animals regularly consumed for the direction of seasonal and annual population trends seemed to continue unchanged by the pressure of fox predation.

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## APPENDIX

TABLE A. Numbers of individual food items located in the field.

	Period I June 1938- June 1939	Period II June 1939- June 1940	Period III June 1940- June 1941
<i>Bufo americanus</i> .....	1		
<i>Gallus gallus</i> .....	2	5	2
<i>Colinus virginianus</i> .....	.	2	
<i>Phasianus colchicus</i> .....	2	2	1
<i>Zenaidura macroura</i> .....	.	.	1
<i>Chordeiles minor</i> .....	.	.	1
<i>Corvus brachyrhynchos</i> .....	1	.	
<i>Sitta carolinensis</i> .....	.	.	1
FRINGILLIDAE, undetermined.....	.	.	2
<i>Spizella arborea</i> .....	.	3	
<i>Melospiza georgiana</i> .....	1	.	
 <i>Didelphis virginiana</i> .....	.		1
<i>Scalopus aquaticus</i> .....	1	4	5
<i>Cryptotis parvus</i> .....	.	1	1
<i>Blarina brevicauda</i> .....	1	3	
<i>Procyon lotor</i> .....	.	1	
<i>Mustela frenata</i> .....	.	1	1
<i>Mustela vison</i> .....	.	.	1
Rodent, undetermined.....	1		
<i>Peromyscus</i> spp.....	4	3	2
<i>Microtus</i> sp.....	7	3	1
<i>Sylvilagus floridanus</i> .....	9	20	8
<i>Bos taurus</i> .....	1	.	
<i>Sus scrofa</i> .....	.	1	1
 Acorns, <i>Quercus</i> sp. ....	.	1*	

\*An undetermined number of acorns were scratched out of the snow and eaten. Much "sign" of foxes was also seen about trees bearing fruit that was appearing in the fecal passages, and although there was no question but that the foxes were eating the fruit the "sign" did not show it.

TABLE B. Occurrences of food remains in 12 fecal passages collected at a rearing den in May, 1939.

Classification of Items	
<b>MAMMALS.</b>	12
<b>RODENTS.</b>	5
Undetermined	2
Determined	3
<i>Microtus</i>	2
<i>Peromyscus</i>	2
<b>RABBITS.</b>	11
<i>Sylvilagus floridanus</i>	11
<b>BIRDS.</b>	8
Undetermined	2
Determined	6
<b>NONNAME.</b>	6
<b>GALLIFORMES</b>	1
<i>Gallus gallus</i>	1
<b>PICIFORMES</b>	1
<b>PASSERIFORMES</b>	1
Undetermined	2
Determined	2
<b>FRINGILLIDAE</b>	2
<b>INSECTS.</b>	12
<b>ORTHOPTERA</b>	2
<b>GRYLILDAE</b>	2
<i>Gryllus assimilis</i>	2
<b>LEPIDOPTERA</b>	1
<b>COLEOPTERA</b>	1
<b>CARABIDAE</b>	9
Undetermined (1 larva)	1
Determined	8
<i>Calosoma calidum</i>	1
<i>Calosoma scrutator</i>	1
<i>Evarthrus colossus</i>	1
<b>SCARABAEIDAE</b>	1
<i>Geotrupes</i>	1
<i>Phyllophaga</i>	1

TABLE C. Occurrences of animal remains in fecal passages collected at rearing dens in 1940.

	APRIL		MAY		JUNE
	SEC. RUN FAMILY So. Range, Dens 1, 2, 3 April 7 to 30	CYCLONE CR. FAMILY No. Range, Dens 1, 2, 3 April 5 to 28	SEC. RUN FAMILY So. Range, Dens 4, 5 May 1 to 29	CYCLONE CR. FAMILY No. Range, Dens 3, 4 May 7 to 31	SEC. RUN FAMILY So. Range, Dens 6 June 1 to 8-10
No. Fecal Passages	34	83	16	73	16
MAMMALS	34	83	14	75	13
Undetermined	1	1	1	1	1
Determined	20	..	..	..	..
INSECTIVORES	..	1	..	1	2
<i>Scalopus aquaticus</i>	..	1	..	..	2
<i>Blarina brevicauda</i>	..	..	..	1	..
CARNIVORES	1	..	..	..	..
CANIDAE	1	..	..	..	..
RODENTS	25	47	3	30	3
Undetermined	6	4	1	2	..
Determined	14	43	1	28	..
<i>Citellus tridecemlineatus</i>	..	..	..	1	..
<i>Tamias striatus</i>	..	2	..	1	1
<i>Sciurus niger</i>	..	..	..	2	..
<i>Reithrodontomys megalotis</i>	1	6	..	..	..
<i>Peromyscus</i>	4	13	1	15	..
<i>Synaptomys cooperi</i>	1	..	1	2	1
<i>Microtus</i>	16	24	1	10	2
<i>Rattus norvegicus</i>	..	2	..	..	..
RABBITS	19	75	13	69	11
<i>Sylvilagus floridanus</i>	19	75	13	69	11
HOOFED MAMMALS	..	5	..	1	..
<i>Sus scrofa</i>	..	5	..	1	..
BIRDS	11	34	9	27	2
Undetermined	4	18	..	10	..
Determined	7	16	..	17	..
NONGAME	6	16	..	13	..
GALLIFORMES	..	1	..	..	..
<i>Gallus gallus</i>	..	1	..	..	..
STRIGIFORMES	..	3	..	..	..
PASSERIFORMES	6	10	..	13	..
Undetermined	2	..	..	12	..
Determined	1	..	..	4	..
FRINGILLIDAE	1	..	..	4	..
GAME	1	..	..	5	..
GALLIFORMES	..	..	..	5	..
<i>Phasianus colchicus</i>	..	..	..	5	..
COLUMBIFORMES	1	..	..	..	..
<i>Zenaidura macroura</i>	1	..	..	..	..
MAY					
	SEC. RUN FAMILY So. Range, Dens 4, 5 May 1 to 29-31	CYCLONE CR. FAMILY No. Range, Dens 3, 4 May 7-30		SEC. RUN FAMILY So. Range, Den 6 June 1 to 8-10	
No. Fecal Passages	16	..	73	..	16
INVERTEBRATES	15	..	61	..	15
DIPLOPODS	..	..	1	..	..
INSECTS	15	..	61	..	15
Undetermined	..	..	2	..	..
Determined	..	..	45	..	4
ORTHOPTERA	..	..	12	..	1
ACRIDIDAE	..	..	..	..	1
<i>Amblo</i>	..	..	..	..	1

TABLE C (Continued)

	MAY		JUNE		
	SEC. RUN FAMILY So. Range, Dens 4, 5 May 1 to 29-31	CYCLONE CR. FAMILY No. Range, Dens 3, 4 May 7-30	SEC. RUN FAMILY So. Range, Den 6 June 1 to 8-10		
No. Fecal Passages..	16	73	16		
GRYLLIDAE.....		12	4		
<i>Gryllus assimilis</i> .....		12	4		
LEPIDOPTERA.....	3	4	5		
DIPTERA.....	1	3	..		
COLEOPTERA.....	15	58	15		
CARABIDAE.....	10	40	10		
Undetermined.....	5	21	4		
Determined.....	8	29	8		
<i>Calosoma</i> spp.....	13	26	10		
<i>Pasimachus elongatus</i> .....		1	..		
<i>Dicaelus sculptilis</i> .....		2	..		
<i>Scartes</i> .....		1	..		
<i>Pterostichus</i> .....		2	..		
<i>Evarthrus</i> .....	1	9	1		
<i>Chlaenius</i> .....	2	5	1		
<i>Harpalus caliginosus</i> .....		3	..		
<i>Harpalus pleuriticus</i> .....		1	..		
SILPHIDAE.....		1	..		
STAPHYLINIDAE.....		3	..		
TENEBRIONIDAE.....		1	..		
SCARABAEIDAE.....	15	46	15		
Undetermined.....		1	..		
Determined.....		46	..		
<i>Copris anaglypticus</i> .....	2	..	..		
<i>Trox</i> .....	1	..	..		
<i>Aphodius</i> .....		1	..		
<i>Phyllophaga</i> .....	15	46	15		
CHRYSOMELIDAE.....		1	..		
HYMENOPTERA.....	5	8	2		
FORMICIDAE.....	5	8	1		
ANDRENIDAE.....		..	1		

TABLE D. Differences in occurrences of animal and plant remains in fecal passages from the trails on the North and South Ranges, 1940.

	APRIL 1-23		APRIL 23- JUNE 20		JUNE 20- JULY 31		AUGUST	
	S.	N.	S.	N.	S.	N.	S.	N.
Ranges.....	12	21	21	35	33	74	10	16
No. Fecal Passages.....	12	21	21	37	50	102	16	20
MAMMALS.....	12	21	21	35	33	74	10	16
Undetermined.....		2	..	..	4	..	..	..
Determined.....		20	..	..	29	..	..	..
INSECTIVORES.....		1	2	1	8	11	1	2
<i>Scalopus aquaticus</i> .....		2	1	8	10	1	1	..
<i>Blarina brevicauda</i> .....		1	..	..	1	..	1	..
RODENTS.....	7	14	9	13	10	40	6	11
Undetermined.....	1	..	..	1	2	5	3	2
Determined.....	6	..	..	13	8	35	4	9
<i>Marmota monax</i> .....		..	..	..	1	..	..	..
<i>Citellus tridecemlineatus</i> .....		..	..	..	1	3	..	1
<i>Citellus franklini</i> .....		..	..	..	..	..	1	..
<i>Tamias striatus</i> .....		..	..	2	2	4	..	3
<i>Sciurus niger</i> .....	1	2	1	2	1	5	2	..
<i>Glaucomys volans</i> .....		..	1	..	..	..	..	..
<i>Reithrodontomys megalotis</i> .....		3	..	2	..	1	..	..

TABLE D (Continued)

	APRIL 1-23		APRIL 23- JUNE 20		JUNE 20- JULY 31		AUGUST	
	S.	N.	S.	N.	S.	N.	S.	N.
Ranges.....	21	37	50	102	16	20		
No. Fecal Passages.....	21	37	50	102	16	20		
INVERTEBRATES.....	10	20	45	89	14	17		
DIPLOPODS.....	1	..	..	..	..	..		
INSECTS.....	10	20	45	89	14	17		
ORTHOPTERA.....	1	3	11	53	10	11		
ACRIDIDAE.....	..	..	1	9	8	10		
TETTIGONIDAE.....	..	..	..	..	..	1		
GRYLLIDAE.....	1	3	11	48	..	2		
<i>Gryllus assimilis</i> .....	1	3	11	48	..	2		
HEMIPTERA.....	1	..	..	..	..	..		
Homoptera.....	..	..	..	..	..	1		
ODONATA.....	..	..	..	..	..	..	1	
LEPIDOPTERA.....	2	..	..	..	1	..	1	
DIPTERA.....	..	..	..	..	1	..	1	
COLEOPTERA.....	9	19	44	75	10	14		
Undetermined.....	1	..	4	4	..	..		
Determined.....	8	..	43	75	..	..		
CARABIDAE.....	5	14	13	41	1	3		
Undetermined.....	2	7	8	15	1	2		
Determined.....	4	12	8	31	..	1		
<i>Calosoma</i> spp.....	4	11	6	26	..	1		
<i>Elaphrus ruficollis</i> .....	..	..	1	..	..	..		
<i>Pasimachus elongatus</i> .....	1	..	..	..	..	..		
<i>Scartes</i> .....	..	2	..	..	1	..		
<i>Evarthrus</i> .....	1	..	1	1	1	..		
<i>Chlaenius</i> .....	..	3	..	..	..	..		
<i>Harpalus caliginosus</i> .....	..	..	..	5	..	..		
HYDROPHILIDAE.....	1	..	..	..	..	..		
STAPHYLINIDAE.....	..	..	..	..	1	..		
ELATERIDAE.....	..	..	..	..	2	..		
EROTYLIDAE.....	..	..	..	..	..	1		
SCARABAEIDAE.....	5	20	19	30	9	13		
Undetermined.....	..	1	..	2	..	1		
Determined.....	..	20	..	28	..	12		
<i>Copris anaglypticus</i> .....	..	1	..	..	1	..		
<i>Aphodius</i> .....	..	1	..	..	..	..		
<i>Bolbocerasoma faretum</i> .....	1	..	..	..	5	4		
<i>Geotrupes</i> .....	..	..	..	..	7	9		

TABLE D (Continued)

	APRIL 23- JUNE 20		JUNE 20- JULY 31		AUGUST	
	S.	N.	S.	N.	S.	N.
Ranges.....						
No. Fecal Passages.....	21	37	50	102	16	20
<i>Phyllophaga</i> .....	4	19	18	19	1	1
<i>Pelidnota punctata</i> .....			1	1		
<i>Ligyrus gibbosus</i> .....	1	1		7		
<i>Xyloryctes satyrus</i> .....				2		
<i>Euphoria inda</i> .....		1				
LUCANIDAE.....	1	..	35	32	1	..
<i>Lucanus</i> .....	1	..	35	32	1	..
<i>Dorcus</i> .....			1	1		
HYMENOPTERA.....	2	..	5	4		3
FORMICIDAE.....	2	..	5	4		3
	APRIL 1-23		APRIL 23- JUNE 20		JUNE 20- JULY 31	
	S.	N.	S.	N.	S.	N.
Ranges.....						
No. Fecal Passages.....	12	21	21	37	50	102
PLANTS.....		2	2	8	28	90
GRAMINEAE- CYPERACEAE.....			4	1	3	..
<i>Zea mays</i> .....		1	..	..	..	1
<i>Quercus</i> .....			1			
<i>Ulmus</i> .....		2	3	2	..	
<i>Morus rubra</i> .....				17	83	2
<i>Grossularia</i> spp.....				6	15	2
<i>Amelanchier canadensis</i> .....				13	2	1
<i>Prunus americana</i> .....				..	2	4
<i>Padus virginiana</i> .....					10	10

TABLE E. Mammal remains in fecal passages from the trails.

TABLE E (Continued)

No. Fecal Passages Period II, June 1939-June 1940...	June	July	August	September	October	November	December	January	February	March	April	May
	25	33	74	60	47	22	34	47	19	36	60	58
Determined . . . . .	14	18	49									57
INSECTIVORES . . . . .			1		1							1 3
<i>Scalopus aquaticus</i> . . . . .			1		1							1 2
<i>Blarina brevicauda</i> . . . . .												1
CARNIVORES . . . . .								1				
<i>Taxidea taxus</i> . . . . .								1				
RODENTS . . . . .	4	6 28	34 33	20 22	14	12 17	30	27				
Undetermined . . . . .		1	2 4	2 1	3	2 1	1	1	1	1		
Determined . . . . .		5 26	31 31	19 19	12	11	16	29	25			
<i>Marmota monax</i> . . . . .									1			1
<i>Citellus tridecemlineatus</i> . . . . .					1							
<i>Tamias striatus</i> . . . . .			2	3								
<i>Sciurus niger</i> . . . . .		2		2	1	1	1					3 3
<i>Glaucomys volans</i> . . . . .												1 1
<i>Reithrodontomys megalotis</i> . . . . .						4	1	1	2			3 3
<i>Peromyscus</i> spp. . . . .	3	2	7	9	6	8	6	7	6	11	7	
<i>Synaptomyss cooperi</i> . . . . .			4	1	5	1			1	4	2	1
<i>Microtus</i> spp. . . . .	4	2	18	24	23	14	11	5	4	11	13	11
<i>Mus musculus</i> . . . . .	1					1	1	1	1			
<i>Rattus norvegicus</i> . . . . .							2					1 1
RABBITS . . . . .	13	15 42	26 32	14	26	41	16	26	47	47	48	
Undetermined . . . . .												1
Determined . . . . .												27
<i>Sylvilagus floridanus</i> . . . . .	13	15 42	26 32	14	26	41	16	27	47	48		
HOOFED MAMMALS . . . . .												5
<i>Sus scrofa</i> . . . . .												5
No. Fecal Passages Period III, June 1940-June 1941...	47	127	43	57	39	30	37	23	19	33	20	
MAMMALS . . . . .	40	87	31	31	38	30	36	22	19	33	18	
Undetermined . . . . .		1	3	2			1					1
Determined . . . . .		39	84	29			35					17
MARSUPIALS . . . . .												3
<i>Didelphis virginiana</i> . . . . .												3
INSECTIVORES . . . . .	4	16	3		1				1	1	1	
<i>Scalopus aquaticus</i> . . . . .	4	15	2									
<i>Cryptotis parvus</i> . . . . .						1			1			
<i>Blarina brevicauda</i> . . . . .		1	1						1			
CARNIVORES . . . . .					3	1		1	1			1
<i>Procyon lotor</i> . . . . .									1			
<i>Mustela</i> . . . . .						3						1
<i>Mephitis mephitis</i> . . . . .												1
<i>Taxidea taxus</i> . . . . .							1					
RODENTS . . . . .	15	42	21	25	33	22	18	13	8	21	7	
Undetermined . . . . .		3	6	5	1	1	2	1				
Determined . . . . .		13	37	17	24	32	20	17				
<i>Marmota monax</i> . . . . .		3					2					
<i>Citellus</i> sp. . . . .					1							
<i>Citellus tridecemlineatus</i> . . . . .				4	2							
<i>Citellus franklini</i> . . . . .				1			1					
<i>Tamias striatus</i> . . . . .		3	5	4	8	1						
<i>Sciurus niger</i> . . . . .		6	3		2	2	5	1	1	3	1	
<i>Reithrodontomys megalotis</i> . . . . .				1		1	3	1	3		3 2	
<i>Peromyscus</i> spp. . . . .	3	10	3	4	20	7	8	3		6	2	
<i>Synaptomyss cooperi</i> . . . . .		3		1	4		1	1				
<i>Microtus</i> spp. . . . .	6	15	7	14	14	12	11	8	7	14	3	
<i>Ondatra zibethica</i> . . . . .									1			
<i>Mus musculus</i> . . . . .								1				
<i>Rattus norvegicus</i> . . . . .				1	1	1	1					1
RABBITS . . . . .	27	42	13	10	22	24	30	20	19	26	14	
<i>Sylvilagus floridanus</i> . . . . .	27	42	13	10	22	24	30	20	19	26	14	
HOOFED MAMMALS . . . . .							2	2	2			
<i>Sus scrofa</i> . . . . .							2	2	1			
<i>Odocoileus virginianus</i> . . . . .									1			

TABLE F. Bird remains occurrences in fecal passages from the trails.

No. Fecal Passages	June	July	August	September	October	November	December	January	February	March	April	May
Period I, June 1938-June 1939	3	5	28	19	12	17	35	32	13	50	22	12
<b>BIRDS</b>	<b>1</b>	<b>1</b>	<b>17</b>	<b>5</b>	<b>3</b>	<b>3</b>	<b>5</b>	<b>6</b>	<b>9</b>	<b>15</b>	<b>8</b>	<b>6</b>
Undetermined				1	2	2		3	2	3	2	1
Determined				1	16	5	1	1	3	7	12	6
NONGAME				1	16	5	1	4	2	7	9	6
Undetermined						1						
Determined				1	4							
GALLIFORMES				1	15	4		3	2	1	7	1
<i>Gallos gallus</i>				1	15	4		3	2	1	7	1
PASSERIFORMES				2			1		6	2	5	1
PICIFORMES					1		1					1
PASSERIFORMES				2			1		6	2	5	1
Undetermined					1						2	1
Determined											3	1
<i>Junco hiemalis</i>						1				6	2	3
<i>Spizella arborea</i>									3			1
GAME				1			1	1	1	3		1
GALLIFORMES				1				1	1	3		1
<i>Colinus virginianus</i>								1				
<i>Phasianus colchicus</i>				1					1	1	2	
COLUMBIFORMES						1						
<i>Zenaidura macroura</i>						1						
No. Fecal Passages												
Period II, June 1939-June 1940	25	33	74	60	47	22	34	47	19	36	60	58
<b>BIRDS</b>	<b>1</b>	<b>5</b>	<b>15</b>	<b>17</b>	<b>14</b>	<b>7</b>	<b>18</b>	<b>20</b>	<b>5</b>	<b>12</b>	<b>24</b>	<b>31</b>
Undetermined		1	7	5	4	1	2	6	3	5	11	17
Determined		4	8	13	10	6	16	14	2	7	14	18
NONGAME		3	7	12	9	6	15	12	1	6	12	14
Undetermined			2		1							4
Determined			5	8								10
GALLIFORMES			2	3	9	5	2	8			4	5
<i>Gallos gallus</i>			2	3	9	5	2	8			4	5
STRIGIFORMES			1									
<i>Asio or Bubo</i>			1									
PICIFORMES					1							1
<i>Dryobates villosus</i>												1
PASSERIFORMES						1	1	1	1			3
PICIFORMES						1	1	1	1			3
PASSERIFORMES			1	1	2	4	3	6	12	1	2	4
Undetermined						2	2	5	2			6
Determined						2	1	2	10			3
CORVIDAE												
<i>Cyanocitta cristata</i>									1			
TURDIDAE						1						
<i>Turdus</i>												
<i>migratorius</i>						1						
ITERIDAE												2
<i>Sturnella</i>												2
PLOCEIDAE						1						
<i>Passer domesticus</i>							1					
FRINGILLIDAE					2	1		2	10			1
Undetermined								1	4			
Determined								1	6			
<i>Junco hiemalis</i>								1	2			
<i>Spizella arborea</i>									4			
<i>Spinus tristis</i>						2						
GAME					1	1	1	1	1	2	1	3
GALLIFORMES					1	1		1	2	1	1	3
<i>Colinus virginianus</i>								1	1	1	1	2
<i>Phasianus colchicus</i>					1	1		1	1	1	1	2
COLUMBIFORMES						1	1					
<i>Zenaidura macroura</i>							1					

TABLE F (Continued)

No. Fecal Passages	June	July	August	September	October	November	December	January	February	March	April	May
Period III, June 1940-June 1941.	47	127	43	57	39	30	37	23	19	33	20	
<b>BIRDS</b>												
Undetermined	18	22	4	9	14	17	20	2	3	11	1	
Determined	17	11		6	5	6	9		2	6	4	
<b>NONGAME</b>												
Undetermined	1	11		3	9	11	11		1	5	3	
Determined	1	9	4	2	8	11	4	1	1	5	2	
<b>GALLIFORMES</b>												
<i>Gallus gallus</i>	5	3	1	6	5					2	2	
<i>Guinea fowl</i>	5	3	1	6	2					2	2	
<b>STURNIFORMES</b>												
<b>PASSERIFORMES</b>	1	4	1	1	2	6	4			3		
Undetermined		2										
Determined		2										
<b>CORVIDAE</b>												
<i>Cyanocitta cristata</i>												
<b>PARIDAE</b>												
<i>Penthestes atricapillus</i>												
<b>FRINGILLIDAE</b>												
Undetermined	2			1	6	3				3		
Determined							2	1				
<i>Richmondena cardinalis</i>							4	2				
<i>Juncos hiemalis</i>									1			
<b>GAME</b>									1	4	1	
<b>GALLIFORMES</b>									1	7	1	
<i>Phasianus colchicus</i>	2									7	1	
<b>COLUMBIFORMES</b>										1		
<i>Zenaidura macroura</i>	1								1			

TABLE G. Occurrences of invertebrate remains in fecal passages from the trails.

No. Fecal Passages Period I, June 1938-June 1939	June	July	August	September	October	November	December	January	February	March	April	May
	3	5	28	19	8	6	2	11	3	9		
<b>INSECTS</b>	3	4	28	19	8	6	2	11	3	9		
Undetermined											1	
Determined											2	
ORTHOPTERA	1	3	26	19	8	5				3		2
ACRIDIDAE	1	2	26	19	8	5				3		
Undetermined										1		
Determined										2		
<i>Hippiscus rugosus</i>							1					
<i>Diastosteira carolina</i>			1	3								
<i>Trachyrachis k. kiowa</i>					1							
<i>Melanoplus</i>	1	2	26	18	8	4				2		
TETRIGONIIDAE			2	2								
GRYLILIDAE				1							2	
<i>Gryllus assimilis</i>				1							2	
HEMIPTERA					1		1	1	1	1		
EPHEMEROPTERA											1	
LEPIDOPTERA		1	3	2								4
DIPTERA			8	3								
COLEOPTERA	3	4	21	15	3	2	1	7	7	9		
Undetermined					2					5		
Determined					15	3	2		2	8		
CICINDELIDAE		1										
CARABIDAE	1	4	6	8	2	2				1	5	
Undetermined		2	3	6	1					1		
Determined		3	3	5	1	2				5		
<i>Caenibus</i>											3	
<i>Calosoma</i> spp.					1		2				4	

TABLE G (Continued)

TABLE G (Continued)

TABLE H. Plant remains in fecal passages from the trails.

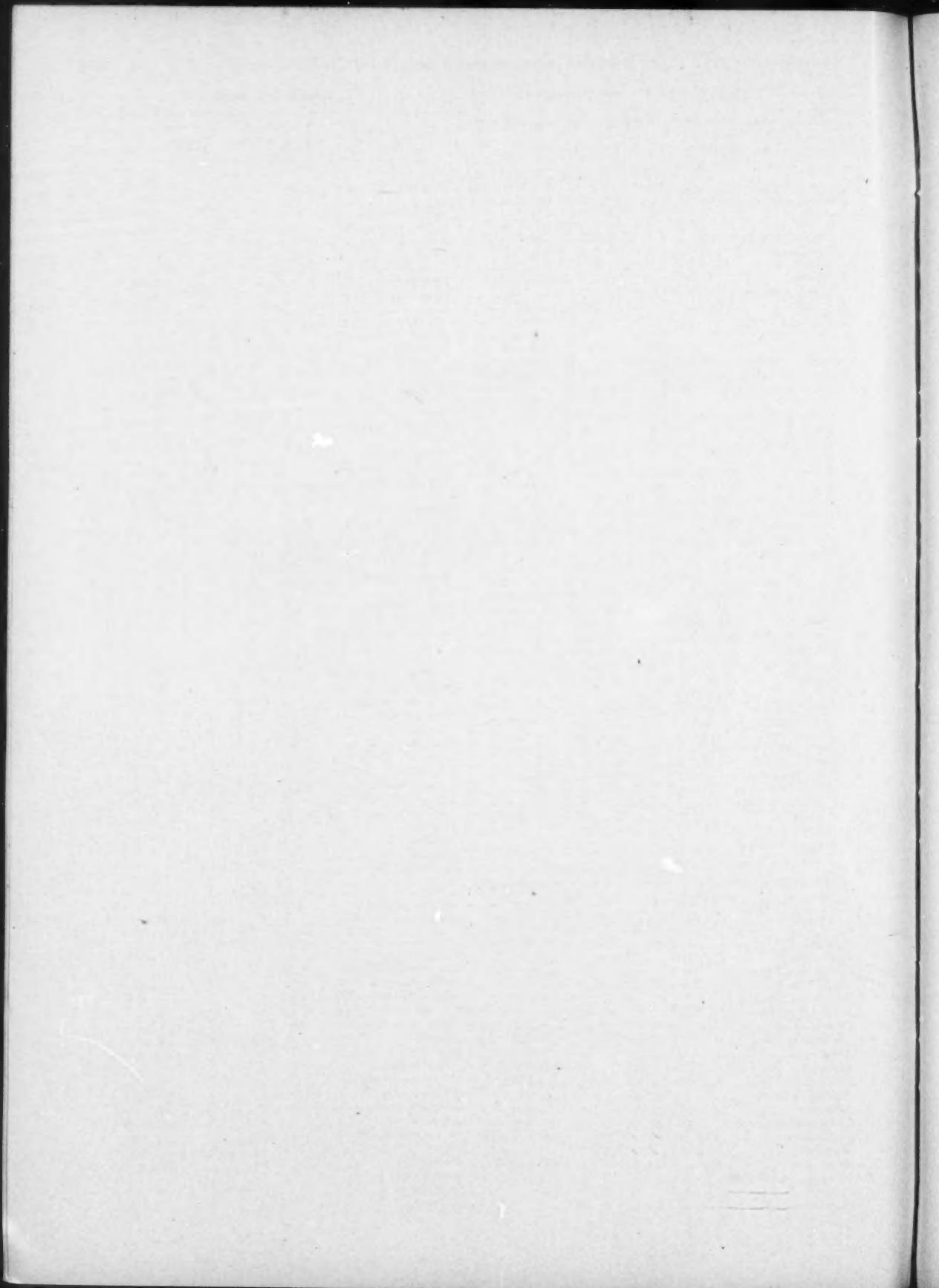
	June	July	August	September	October	November	December	January	February	March	April	May	
No. Fecal Passages													
Period I, June 1938-June 1939	3	5	28	19	12	17	35	32	13	50	22	12	
PLANTS													
GRAMINEAE-CYPERACEAE													
<i>Zea mays</i>													
<i>Quercus</i>													
<i>Rosa</i> sp.													
<i>Nepeta</i> , prob. <i>Cataria</i>													
<i>Physalis</i>													
<i>Solanum nigrum</i>													
<i>Solanum carolinense</i>													
No. Fecal Passages													
Period II, June 1939-June 1940	25	33	74	60	47	22	34	47	19	36	60	58	
PLANTS													
GRAMINEAE-CYPERACEAE													
<i>Zea mays</i>													
<i>Avena sativa</i>													
<i>Quercus</i>													
<i>Grossularia</i> spp.													
<i>Amelanchier canadensis</i>													
<i>Prunus americana</i>													
<i>Padus virginiana</i>													
<i>Vitis vulpina</i>													
<i>Nepeta</i> , prob. <i>Cataria</i>													
<i>Solanum nigrum</i>													
No. Fecal Passages													
Period III, June 1940-June 1941	47	127	43	57	39	30	37	23	19	33	20		
PLANTS													
GRAMINEAE-CYPERACEAE													
<i>Zea mays</i>													
<i>Avena sativa</i>													
<i>Quercus</i>													
<i>Ulmus</i>													
<i>Morus rubra</i>													
<i>Grossularia</i> spp.													
<i>Malus ioensis</i>													
<i>Amelanchier canadensis</i>													
<i>Prunus americana</i>													
<i>Padus virginiana</i>													
<i>Vitis vulpina</i>													
<i>Nepeta</i> , prob. <i>Cataria</i>													
<i>Physalis</i>													
<i>Solanum nigrum</i>													
<i>Solanum carolinense</i>													

TABLE I. Non-food seed occurrences.

No. Fecal Passages	Summer	Fall	Winter	Spring
Period I, June 1938-June 1939	36	48	80	84
<i>Zea mays</i>	1	1	..	..
<i>Syntherisma</i>		3	..	..
<i>Syntherisma Ischaemum</i>		4	3	1
<i>Syntherisma sanguinale</i>	2	7	6	1
<i>Echinocloa Crus-galli</i>		4	1	1
<i>Panicum capillare</i>		2	..	..
<i>Chaetochloa glauca</i>	8	16	11	2
<i>Chaetochloa viridis</i>	3	2	1	1
<i>Avena sativa</i>	1	..	..	..
<i>Eragrostis</i>		..	1	..
<i>Poa Wolfii</i>		1	..	..
<i>Triticum aestivum</i>	1	..	..	..
<i>Carex</i> sp.		1	..	..
<i>Ostrya virginiana</i>	1	..	..	..
<i>Cannabis sativa</i>	1	1	..	..
<i>Rumez</i> sp.		1	..	..
<i>Rumez Actaea</i>		..	1	..
<i>Persicaria pennsylvanica</i>		..	1	..
<i>Persicaria Persicaria</i>		..	2	..
<i>Chenopodium album</i>	2	1	2	..

TABLE I (Continued)

No. Fecal Passages	Summer	Fall	Winter	Spring
Period I, June 1938-June 1939	36	48	80	84
<i>Geum canadense</i>	..	..	2	..
<i>Meibomia</i> sp.	..	1	..	..
<i>Acer</i> sp.	1	..	..	..
<i>Hibiscus Trionum</i>	1	..	..	..
<i>Sanicula marylandica</i>	..	1	1	1
<i>Lappula echinata</i>	2	1	..	1
<i>Verbena hastata</i>	..	2	..	..
<i>Verbena stricta</i>	..	1	..	..
<i>Ambrosia trifida</i>	1	1	1	..
<i>Ambrosia elatior</i>	..	6	5	..
<i>Bidens</i>	..	1	1	..
No. Fecal Passages				
Period II, June 1939-June 1940	132	129	100	154
<i>Juniperus virginiana</i>	..	..	..	1
<i>Syntherisma Ischaemum</i>	..	10	1	..
<i>Syntherisma sanguinale</i>	1	22	11	2
<i>Echinocloa Crus-galli</i>	..	..	2	3
<i>Panicum</i> sp.	..	1	..	..
<i>Panicum capillare</i>	..	1	..	..
<i>Chaetochloa glauca</i>	1	15	5	8
<i>Chaetochloa viridis</i>	..	5	3	2
<i>Cenchrus</i>	..	1	..	1
<i>Calamagrostis</i> sp.	..	..	1	..
<i>Eragrostis</i>	..	1	..	..
<i>Poa</i>	..	1	1	..
<b>CYPERACEAE</b>	..	..	..	1
<i>Cyperus</i> sp.	..	..	1	..
<i>Eleocharis obtusa</i>	..	1	..	..
<i>Carex</i> sp.	..	1	..	..
<i>Ostrya virginiana</i>	..	1	..	..
<i>Cannabis sativa</i>	..	4	..	1
<i>Rumez Actaea</i>	1	..	..	1
<i>Torula virginiana</i>	..	..	1	..
<i>Persicaria</i>	..	1	..	..
<i>Persicaria pennsylvanica</i>	2	1	1	..
<i>Persicaria Persicaria</i>	..	..	2	..
<i>Amaranthus retroflexus</i>	..	..	1	..
<i>Geum canadense</i>	1	2	3	1
<i>Meibomia</i> sp.	..	1	..	..
<i>Rhus glabra</i>	..	1	..	..
<i>Acer</i> sp.	..	..	..	1
<i>Tilia</i> sp.	..	..	..	1
<i>Sanicula marylandica</i>	..	1	..	..
<i>Lappula echinata</i>	1	..	7	1
<i>Verbena hastata</i>	..	..	1	..
<i>Verbena stricta</i>	..	1	..	..
<i>Triosteum</i> sp.	..	..	1	..
<i>Ambrosia trifida</i>	..	1	..	..
<i>Ambrosia elatior</i>	..	4	1	7
<i>Bidens</i>	..	2	..	..
No. Fecal Passages				
Period III, June 1940-June 1941	217	126	79	53
<i>Syntherisma</i> sp.	..	..	1	..
<i>Syntherisma Ischaemum</i>	..	4	..	..
<i>Syntherisma sanguinale</i>	..	13	1	..
<i>Echinocloa Crus-galli</i>	..	1	..	..
<i>Chaetochloa glauca</i>	4	8	1	..
<i>Chaetochloa viridis</i>	..	4	1	..
<i>Cenchrus</i>	..	1	1	..
<i>Poa pratensis</i>	1	..	..	..
<i>Cannabis sativa</i>	..	1	..	..
<i>Polygonum Convolvulus</i>	..	1	..	..
<i>Persicaria</i>	..	..	2	..
<i>Persicaria pennsylvanica</i>	..	3	..	..
<i>Amaranthus</i> sp.	..	1	..	..
<i>Sanicula marylandica</i>	..	..	1	..
<i>Lappula echinata</i>	..	1	..	..
<i>Verbena</i> sp.	..	..	1	..
<i>Ambrosia trifida</i>	1	..	..	..
<i>Ambrosia elatior</i>	1	5	1	..
<i>Bidens</i>	2	1	1	..



A COMPARISON OF THE DRAGONFLY FAUNA OF THE LOWER  
DELTA OF THE MISSISSIPPI RIVER WITH THAT OF THE  
MARSHES OF THE CENTRAL GULF COAST

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# A COMPARISON OF THE DRAGONFLY FAUNA OF THE LOWER DELTA OF THE MISSISSIPPI RIVER WITH THAT OF THE MARSHES OF THE CENTRAL GULF COAST

## INTRODUCTION

This paper is the result of several years studies on the Odonata of the marshlands of the deep South. Its main purpose is to compare the dragonfly population of the large areas of established marshes of the Central Gulf Coast with that of the lower active delta of the Mississippi River. In this investigation the Central Gulf Coast includes that region from Grand Isle, Louisiana, eastward to the Alabama-Florida state line, and the lower delta is restricted to that area of the Mississippi delta in which active deposition occurs. This portion of the lower delta begins at Venice, Louisiana, and extends to the Gulf of Mexico (Fig. 1). The species of dragonflies found in the two areas are listed and a comparison of the populations is given.

The writer's interest in the study of dragonflies was aroused while a student at Tulane University, during the summer of 1932. During the school sessions of 1932-1933 and 1933-1934 and the summer session of 1933 and 1934 I was afforded the privi-

lege of accompanying Drs. Penfound and Hathaway, both of Tulane University, on many of their trips made in connection with their study of marsh ecology (Penfound and Hathaway 1938). Additional collecting trips were taken during the period from 1932 to 1934 to Grand Isle and Cat Island in the Mississippi Sound; to localities on both sides of the Mississippi River with the most distant being sixty miles below New Orleans; to Lake Pontchartrain on many occasions; and along the Mississippi Sound as far east as Biloxi (Fig. 1). The summers of 1935 and 1936 and the winter of 1935-1936 were devoted to studying dragonflies along the Gulf Coast from Biloxi to the Alabama-Florida line, with the major portion of the time being spent in Mobile and Baldwin counties, Alabama. On the average two or three trips were made per week during this time.

In addition, the writer has examined and identified specimens in the collections of Tulane University, the Southern Biological Supply Company, the Louisiana State Museum, and the Normal School, all being located in New Orleans. The writer is indebted

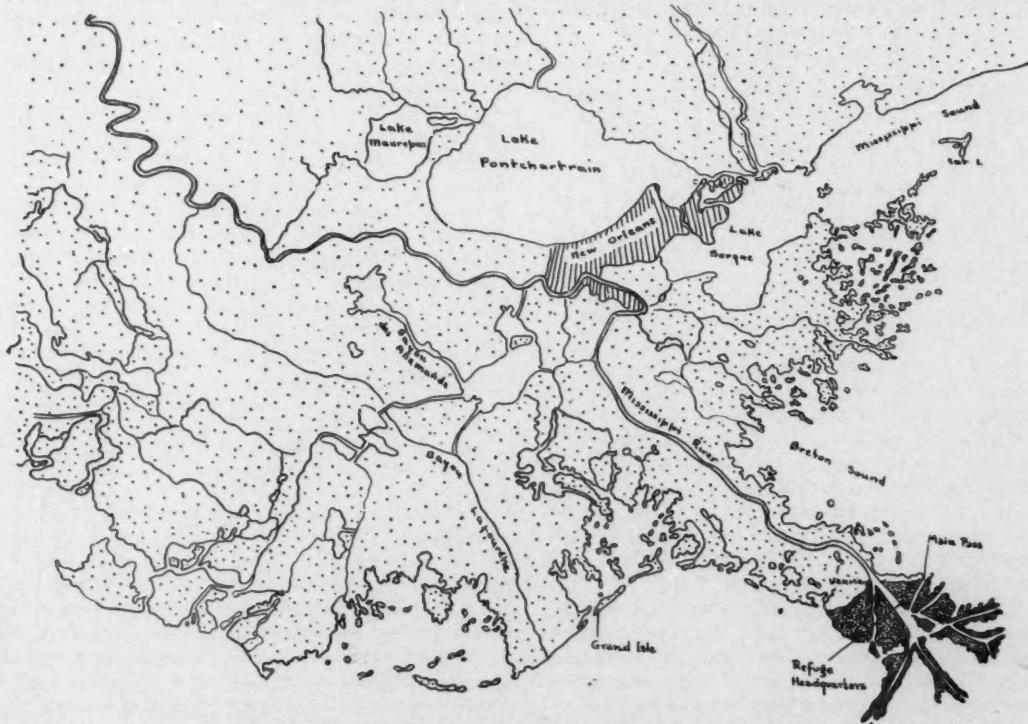


FIG. 1. Portion of Louisiana and Mississippi showing the coastal areas and active delta of the Mississippi River. The heavily shaded area is the active delta.

to these organizations for their permission to examine these specimens. Thanks are also due to the many friends who have so kindly collected specimens in this area and sent them to the writer. With the exception of the few cases mentioned above, all collecting, determining, and field observations were made by the writer.

The writer wishes to express his sincere appreciation to the following persons who have done much to make this study possible: Mr. J. J. Lynch of the United States Fish and Wildlife Service for accompanying the writer throughout the studies in the lower delta, for explanation of the ecology of the area, and for permission to use salinity data collected by him over a long period of time. To Mr. J. H. Sutherlin and Mr. John Kilby, both of the United States Fish and Wildlife Service, for permission to use the laboratory for lodging and for the use of boats for transportation. To Mr. and Mrs. Sutherlin and Mr. and Mrs. Kilby for their very kind hospitality during the studies in the lower delta. To Drs. W. T. Penfound and E. S. Hathaway of Tulane University for arousing the writer's interest in and for his knowledge of coastal marsh ecology. To Dr. W. T. Penfound for very instructive criticism of this manuscript. To Dr. C. H. Kennedy of Ohio State University for many helpful suggestions and criticisms of the manuscript.

#### GENERAL DESCRIPTION OF THE MARSHES OF THE LOWER DELTA OF THE MISSISSIPPI RIVER

This investigation on the Odonata of the lower active delta was confined to the Delta National Wildlife Refuge. This refuge, that covering approximately 90,000 acres, includes the Cubit's Gap System of the Mississippi River, of which Main Pass is the principal distributary. The refuge headquarters are located on the old quarantine island near Pilot Town, Louisiana.

As a result of survey trips in June and July of 1938, thirteen areas already under investigation by Mr. Lynch were selected for intensive study of dragonfly abundance and distribution. Detailed notes and collections were made in these areas during the second week in August, 1938. In no case did we limit our studies to the restricted area of the transect, but at all stations investigation was extended for several hundred yards in all directions. In this way a thorough cross section of the population of the given station was obtained. Supplemental data were obtained by general survey trips over different portions of the area.

During the summer of 1939 two confirmatory trips were taken, the second trip being made in September. Another survey trip was taken during the summer of 1940. In all of these additional trips, observations were made for the greater part along Main Pass and at the various stations on Long Island Bayou. This bayou in its entirety illustrated all of the conditions

found in the lower delta. In order to study the winter conditions in the Delta Refuge, a week and a half was spent there during early March of 1941. Trips were made along Long Island Bayou, Main Pass, and Romere's Pass.

The following notes on physiographic features were obtained from Mr. J. J. Lynch who ably pointed them out to me in the field during my stay in the delta.

In the lower delta, as in the established marshes, the main river distributaries, as a result of the deposition of sediment during floods, form levees along their course. The long delta lobes or fingers, representing these naturally formed levees along the distal portions of the main passes, are characteristic of an active delta. When breaks occur in the levees, the river is allowed to deposit sediment laterally for miles forming what are called subdeltas.

The terminal distributary channels of the river are known as passes. In the subdelta, these passes usually branch and rebranch toward their mouths. Deposition of sediment along the inner banks of a forking pass gives rise, in time, to extended, low levees varying only a few inches in elevation from the edge of the pass to the interior open water area or "bend." These levees are called "flats" as they are only a few inches in elevation above the Gulf level and are subject to inundation by wind tides during the summer. Subsequent deposition causes the elevation of the banks until sufficiently high dikes are formed which all but prohibit deposition in the interior, which remains as open water. Successive bifurcation of the passes eventually results in closure of the bend, thus forming an "outside pond." In the outside pond drainage is prohibited by the closure and, as the summer salt tides which overflow into these areas cannot drain out, the salinity is increased. As the deposition of new land advances gulfward, the ponds become more isolated from salt tides and due to rainfall tend to become fresh again. These isolated fresh ponds are called "inside ponds." The flats, as they become more and more isolated from salt tides by the advancement of the delta, tend to merge, giving rise to areas eventually suitable for permanent marshes.

#### DISCUSSION OF CERTAIN ECOLOGICAL FACTORS IN THE LOWER DELTAIC MARSHES

The area studied, as previously stated, consists of some 90,000 acres located in the subdelta of the Cubit's Gap System. With the exception of the deltaic ridges (the high levees built by deposition along the main river distributaries), the entire region is an aquatic environment, being composed of three general habitat types: areas of flowing water such as passes, ditches, or bayous; the outside and inside ponds, which have lost all connection with the passes; and the marshes. It is probably in order to state here that the term *marsh* is applied to those wet

areas supporting canes, sedges, or grasses, whereas we consider a *swamp* to be a forested area under water.

The permanency of the area is dependent upon the amount and the time of occurrence of rainfall. The high water stage and flood stages of the river occur in the spring and early summer as a result of rains and the melting of the ice at its headwaters. The flooding of the Mississippi River and its passes results in a fresh water inundation of the delta and a transport of fresh water for some distance out into the sounds at its mouth. During the period from July to December the river is at its low water stage. At this time considerable quantities of water are lost from the ponds by evaporation and from the marshes both by evaporation and direct run-off through the natural drainage channels. An examination of Table 1 will show that the greatest amount of rainfall

TABLE 1. Temperature and rainfall data for Lower Mississippi Delta. Monthly mean temperatures and total monthly precipitation were averaged for 22 years from Burwood, La., Weather Bureau Records (Martin and Kincer 1930).

Month	Rainfall (inches)	Temperature ° F.
January	3.90	56.4
February	4.36	56.7
March	3.54	62.5
April	4.04	67.5
May	3.39	75.1
June	3.86	81.4
July	7.18	82.8
August	8.01	82.4
September	6.77	81.2
October	5.58	74.4
November	2.80	64.9
December	4.96	59.1

occurs during this period of low water and thus, during normal years, prevents the drying up of the marshes. The annual average rainfall for this area is 57.22 inches, but it may vary between 38.18 and 81.74 inches (Table 2). An examination of the avail-

TABLE 2. Some climatic factors of the Lower Mississippi River Delta. Taken from data covering a period of 22 years; from Martin and Kincer (1930).

Average annual temperature	70.8° F.
Average annual maximum temperature	77.5° F.
Average annual minimum temperature	64.0° F.
Highest recorded temperature	99.0° F.
Lowest recorded temperature	10.0° F.
Average growing season (estimated)	351 days
Average annual precipitation	57.22 inches
Highest annual precipitation	81.74 inches
Lowest annual precipitation	38.18 inches

able climatic records of the lower delta (Martin & Kincer 1930) show several instances in which the monthly rainfall during this period of low river water did not exceed one inch. These periods of drought would result in the drying up of considerable areas of the marshes.

A still greater effect of the low water period of the river, especially on the aquatic fauna, is the resulting change in salinity. When the spring floods occur the marshes are covered by fresh water and their salinities approach that of fresh water itself. But with the fall of the river in late summer and autumn, the sea water from the Gulf of Mexico invades and inundates the marshes, thus greatly increasing the salinity. Table 3 shows the salinity

TABLE 3. Salinities at transects studied in Lower Mississippi Delta. Salinities expressed in percentage of sea water. These data were obtained through the kindness of Mr. J. J. Lynch, Delta National Wildlife Refuge.

Station	NORMAL		Resulting from storms
	During fresh water in- undation	During salt water in- undation	
Head of Main Pass.....	0	30	70
Johnny Johnson's Bayou.....	0	10	10
Romere's Pass.....	0	40	70
Big Bucket Pond.....	0	25	40
Long Island Bayou.....	0	10	10
Transect No. 1			
Long Island Bayou.....	10	30	40
Transect No. 2			
Long Island Bayou.....	10	40	40
Transect No. 3			
Long Island Bayou.....	10	50	60
Transect No. 4			
Long Island Bayou.....	20	60	70
Transect No. 5			

variations at nine of the stations used in this study. These data were determined by Mr. J. J. Lynch over a considerable period of time. That the salinities are not greater during this salt-water inundation is due to the fact that, as shown above, the rainfall is heaviest during the period from July to December. This tends to appreciably dilute the salt water and accounts for the readings given in Table 3. During times of severe squalls or hurricanes, which are especially prevalent during the late summer, the salt water from the Gulf is driven into the marshes and passes. At such times the salinities reach considerable proportions (Table 3).

The average monthly temperature (over a period of 22 years) of the lower delta is given in Table 1. Table 2 gives the average minimum and maximum and highest and lowest temperature during the same period. The range in normal monthly temperatures from summer to winter is less than 30° F. Such temperatures are excellent for plant growth, the average growing season over the period of 22 years being 351 days. Since the aquatic habits of this area, with the exception of the larger passes which are themselves lotic in nature, are shallow, the temperature of the water therein approximates in general that of the air. During the period of low water, however, due to excessive evaporation, the water level of the marshes may become considerably reduced. In some areas this shallowness of the water

together with the black, mucky bottom, which is the source of heat radiation, results in the marsh water becoming almost superheated. Dense vegetation, when present, and sufficient precipitation serve to overcome this. On the whole, the air and water temperatures in the lower delta are ideal for dragonflies.

The turbidity of the river and the deposition of sediment have very important effects upon the vegetation of this region. The most important effect, from our viewpoint, is the failure of true aquatic plants to survive in any area of the delta invaded by the turbid waters of the river and its passes. The presence of such plants as *Potamogeton* and *Ceratophyllum* in the outside and inside ponds is due to the complete separation of these areas from the silt of the river passes. In addition, those plants which are to be successful in these marshes must be able to overcome the annual deposition, which in some regions reaches as high as 5 to 6 inches per year. The writer has seen specimens of *Scirpus*, from the flats, which illustrate this point. This plant has a horizontal rhizome, which when buried will produce an upward vertical growth until a new horizon level is reached, from which point the normal horizontal growth again occurs. In view of the observation made by Williamson (1903) it is not unlikely that the tremendous sedimentation may prove detrimental in some cases to dragonfly nymphs. Turbidity is occasioned periodically during the summer by the activities of bottom-feeding fishes.

In those areas affected by turbidity there are several plants which the odonate nymphs are able to use for protection against the large numbers of bottom-feeding fishes present in the passes and bayous. Alligator grass (*Achyranthes philoxeroides*) is extremely abundant throughout. It is attached to the banks of the bayous and grows in vast mats out over the water and over portions of the marsh. In many areas these masses of alligator grass are entirely responsible for our being able to walk over the marshes. Such mats afford excellent protection against the larger predators. The writer noted, however, during the winter of 1940-1941, that these mats of alligator grass had been killed back to the shore. The dense stands of various grasses and canes in the marshes and especially around the edges of bents and ponds, also afford good protection.

The protection of the adult dragonflies against the harmful action of rainfall and wind storms is a factor which has not received much attention in the literature. Kennedy (1917) writes, "In the mesophytic east a rainy day during the Odonata season does not seem to affect the numbers of dragonflies on the wing on the succeeding sunny days, but in the dry areas of the west a rainy day will frequently kill nearly all the adults on the wing at the time. I have seen *Ophiogomphus severus* wiped out thus on Sauts Creek, Washington, and *Macromia magnifica* and *Gomphus sobrinus* killed off on Coyote Creek at San Jose, California, by several days of

cold rain, though at the latter place *Libellula saturata* and *Sympetrum ilotum* were apparently not affected. It is possible, though, that the latter were affected, but being all-season species, new adults emerged soon to replace those killed, while in the case of *Macromia magnifica* and *Gomphus sobrinus*, which emerge only during a short season, once being killed, no new ones would appear and so their loss would be noticed." Dr. Kennedy tells me that in those areas in which he noticed the killing off of the dragonflies there was little or no vegetation present.

Our observations in the marshes of the Central Gulf Coast and the lower delta lead us to conclude that vegetation is all important in protecting adult dragonflies against rain and wind. In these marshes the terrific downpouring of rain, which is by no means uncommon, is preceded by the formation of heavy, black storm clouds which result in a darkening and an abrupt drop in temperature in the area covered by them. Upon the advent of these clouds the large numbers of dragonflies that were previously on the wing disappear immediately. Our curiosity aroused, we searched the region in an attempt to discover where the dragonflies were hiding. We found that a number of individuals had taken refuge in wooded areas and in shrubs when present. In the marsh proper, the dense stands of *Phragmites*, *Typha*, *Mariscus*, *Zizaniopsis*, and *Spartina cynosuroides* afforded excellent protection. In the most saline areas, where the canes are usually absent, the honey mangrove and salt marsh grass were used. On very windy days, especially during severe squalls or hurricanes, few dragonflies were observed on the wing. Investigation showed them seeking protection in the same areas noticed during the rain storms.

The only areas throughout the lower delta that can support woods are the deltaic ridges. It is in such regions, undoubtedly, that the shade-loving dragonflies occasionally taken in the marshes are able to survive.

Depth of water is of practically no importance as an inhibiting factor as, with the exception of the river proper and its larger passes, the water is quite shallow. The salt marshes, due to the formation of a peat shelf, are considerably shallower than fresh water marshes. The bottom is composed of sand or clay and is mucky throughout.

Available food for both nymphs and adults is abundant. Throughout the investigation notes were made on the presence and abundance of possible food animals. These records show that copepods were quite abundant and that the fresh water prawn (*Palaemonetes*) was numerous. Young lake shrimp were found in the marsh ponds during the summer, and the postlarvae of the commercial shrimps migrated into the delta during June and thereafter. Chironomid and mosquito larvae were found in large numbers throughout the area. Water beetles, corixids, and leeches were also found. Small fishes, such as *Gambusia* and *Mollinesia*, reach large numbers in some areas. The numbers of mosquitoes, breeding

in both salt and fresh areas, and tabanids in the coastal and deltaic marshes were, undoubtedly, in themselves a sufficiency of food for the adult dragonflies. In addition to these, there were considerable numbers of midges, craneflies, and other insects available. This abundance of food both in the delta and in the coastal marshes is an important factor in the production of such dragonfly populations as were observed in these areas.

Very little information was obtained in regard to predators and parasites in the delta. This refuge is the overwintering area for millions of ducks and thousands of geese annually. These birds, especially the diving ducks, undoubtedly eat considerable numbers of dragonfly nymphs as well as other small aquatic animals. The large numbers of fishes present in the bayous and passes are probably important predators of the nymphs.

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2. *Ischnura posita* Hagen. This species is undoubtedly like *I. ramburii* in being restricted to the vegetated land-locked pools for breeding areas. Its presence at Long Island Bayou Transect No. 5, which is a typical salt marsh, is again probably due to the close proximity of a favorable breeding area. A large number of specimens was obtained at the Refuge Headquarters around drainage ditches and a small pond which afforded excellent breeding places. There is to be constructed in the near future a large pond at the back of the Headquarters which is to be used as a waterfowl banding station. With the proposed propagation of submerged plants, useful as duck food, ideal conditions will be established for the breeding of Zygoptera. In such an event, it would

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quarters, and the head of Main Pass. This species is a shade-loving form and undoubtedly breeds in marshy areas in the wooded levees of the river and the heads of its main passes. It has been noted previously that the only trees present in the lower delta are on the levee ridges. It is not unlikely that the closely related species, *L. incesta* Hagen and *L. axillena* Westwood, may be taken in company with *L. vibrans*. These are not, however, true inhabitants of either the deltaic or coastal marshes.

10. *Cannacia gravida* Calvert. This species was very similar to *Libellula auripennis* in habits, and was found to be as numerous and as widespread as the latter.

11. *Pachydiplax longipennis* Burmeister. Although common in all areas investigated, this species was never found in such great numbers as *Libellula auripennis* and *Cannacia gravida*. From the very first of the investigation, the attention of the writer was drawn to the great variation in size, wing length, and general body size of *P. longipennis*. A series of measurements show in the males a variation in wing length of 28 to 35 mm. and a range in body length from 32 to 45 mm.; in the females wing length from 30 to 42 mm.

In the coastal marshes the writer (1937) noted still larger individuals with a body length of 55 mm. and a wing expanse of 84 mm. These specimens were taken in the vicinity of Mobile, Ala., during the summer of 1935. This considerable size difference was probably due either to the effect of the saline variation upon the nymphs or to a variation in food abundance. Calvert (1929) states, "... starvation, more or less complete, and under appropriate conditions, results in decreased size, prolonged through months or even years, accompanied by moulting, with a progressive diminution in size of the shed skins." In view, however, of the large amount of food available in the delta (see discussion of ecological factors) it would appear that this variation in size was due to some other factor than food.

12. *Erythemis (Mesothemis) simplicicollis* Say. Very abundant and found throughout the entire area during this investigation.

13. *Tramea carolina* Linnaeus. A few specimens of this species were seen along the upper region of Long Island Bayou during September, 1939. *T. carolina*, as in the case of the "darners," has been found by the writer to breed only in fresh or nearly fresh areas. We cannot, with our present knowledge, consider this species as a true inhabitant of the deltaic marshes.

#### GENERAL DESCRIPTION OF THE ESTABLISHED MARSHES OF THE CENTRAL GULF COAST

This region, for our purposes, may be divided into five general habitat types: (1) wooded areas, (2) strictly fresh areas, (3) slightly brackish areas,

(4) brackish areas, and (5) saline areas. In the following discussion of marsh types liberal use has been made of the excellent work of Penfound and Hathaway (1938) on plant communities in the marsh-lands of southeastern Louisiana.

Viosea (1928) states that the marshes of southeastern Louisiana include approximately 1,750,000 acres of fresh water marsh and about 2,500,000 acres of sea marsh. The fresh water marshes occur in large interrupted areas in the interior of the state whereas the saline marshes occupy a practically unbroken strip of coast line several miles in width. Southeastern Louisiana is in general an extensive alluvial plain with little relief which dips slightly toward the Gulf of Mexico and approximates sea level throughout its lower portion. Each stream flowing into this plain is flanked by natural levees which are formed during flood period by the deposition of the coarser sediments. These levees or "front lands" gradually decrease in elevation away from the stream front to the so-called "back lands," which differ from the front lands in the finer texture and darker color of their soils. Where these back lands fall below the mean water table they are occupied by cypress-gum swamps and marshes in fresh water areas but only by marshes in the more saline areas. These back lands, due to the levees, do not drain into the main streams but serve as catch basins for the overflow water and for rainfall in the alluvial plain. Such areas are drained by sluggish, meandering bayous which are characterized by low, insignificant levees. There are occasional elongated or nearly circular areas, usually wooded, which vary from a few inches to several feet above the surrounding marshes. Whenever one of these elevations is covered with evergreen oaks it is termed a "cheniere." The elevation of the area, under the same salt concentrations, is of utmost importance in determining the type of vegetation. This is well attested to by the following statement of Penfound and Hathaway (1938), "It should be emphasized also that the transition from one community to another is conditioned by a change in elevation of as little as three inches, since four communities may occur on a slope having a fall of less than one foot."

The marshes may be classified, on the basis of salinity, into two major groups, fresh areas and salt areas. In the fresh areas the pattern of vegetation is constant: pine or oak forest, cypress-gum swamp, and marsh. There is a lack of zonal communities of shrub, cane, and salt grass. The outstanding feature of the fresh water marshes is the presence of sedges and grasses eight to ten feet in height. Communities of submerged aquatics are present only in the fresh water areas. In the salt water areas the cypress-gum swamp is absent and the pine or oak forest is followed, at successively lower levels, by zones of shrub (*Baccharis* and *Iva*), reed-grass (*Phragmites communis* and *Spartina cynosuroides*), and salt grass (*Distichlis spicata*), beyond which is the marsh. The dominant species of the salt marshes

varying in height from two to four feet are in striking contrast to the towering species of the fresh marshes.

Each of the two major habitat groups is composed of two subtypes which were recognized by the writer by the vegetation peculiar to each:

1. *Strictly fresh areas*—0 percent sea water (0 percent salt). Marsh characterized by the broad-leaf eattail (*Typha latifolia*) and the giant bulrush (*Scirpus californicus*).

2. *Slightly brackish areas*—0 to 14 percent sea water (less than 0.5 percent salt). Marsh composed largely of saw grass (*Mariscus jamaicensis*), although there were usually found several species typical of salt marshes, but only in the lower areas where there was an appreciable amount of salt in the water.

3. *Brackish areas*—14 to 57 percent sea water (0.5 to 2.0 percent salt). The brackish marsh may be composed of a pure stand of couch grass (*Spartina patens*) in less saline areas or of pure stands of black rush (*Juncus roemerianus*) in sandy areas, but there was usually an admixture of one or both of these species with salt grass.

4. *Saline areas*—57 to 143 percent sea water (2.0 to 5.0 percent salt). Saline marshes were dominated by the salt cane (*Spartina alterniflora*) and couch grass was always absent in strongly saline areas. Penfound and Hathaway remark, "Since both black rush and salt grass have wide ranges of salt tolerance which overlap with that of salt cane, the dominant of the saline marsh, the brackish marsh merges insensibly into the saline marsh."

#### DISCUSSION OF CERTAIN ECOLOGICAL FACTORS IN THE MARSHES OF THE CENTRAL GULF COAST

The climatic factors in the established areas are quite favorable for dragonfly production. The average annual temperature (long term average), as typified by the marshes in the vicinity of New Orleans, is 69.4° F., with the mean monthly temperatures of 54.6° F. for January and 82.4° F. for July. The average annual precipitation is 59.34 inches, with the rainfall evenly distributed throughout the year. July and August are the wettest months and October and November are the driest. Penfound & Hathaway (1938) state, "Since there are few severe frosts and since the frostless season (growing season) is 326 days, some species (of plants) are found in bloom every day of the year." Such conditions were in part responsible for the large dragonfly population found in the coastal marshes.

The writer has discussed in some detail certain ecological factors which affect Odonata in the lower deltaic marshes. Since, in general, the majority of these factors exert the same influence upon dragonflies in the established marshes of the Central Gulf Coast, we will concern ourselves here chiefly with those which differ radically in the two areas.

The established marshes of the Gulf Coast differ most radically from the lower deltaic marshes in regard to salinity. The saline marshes form a wide strip along the Gulf coast line and are connected to the large, interrupted, inland areas of fresh marshes by a series of brackish marshes varying in salinity between that of the true saline and the strictly fresh condition. The salinity of any given area may vary considerably, but usually does so within a restricted range which characterizes it. Strictly fresh marshes probably never have more than a slight trace of salt. In the slightly brackish areas, however, the salinity varies within a range of 0 to 0.5 percent salt (0 to 14 percent sea water). Severe storms may increase the salt content by driving in waters from nearby brackish areas. Nowhere in this area, as is found in the lower deltaic marshes, do we find normally fresh regions which have saline concentrations at times approaching that of the true salt marshes. This is due primarily to the lack of a central water distributing system, such as the Mississippi River, which during high water stage spreads fresh water over the marshes and during its low level allows an invasion of salt water. In addition, the normal tides average only about one foot throughout the outlying salt marsh area, and less or none in the interior (Viosea 1926).

The second factor which differs widely in the two areas is that of turbidity. In the coastal established marshes the waters are lacking in turbidity during the greater portion of the year. The mud of the Mississippi drainage does not concern them. It is true that sediment is carried and deposited by the distributing units during their own short high water and flood periods, but this does not last long enough to prohibit the growth of submerged and floating plants. The drainage bayous (Section 5), however, often remain turbid during the major portion of the year. In the coastal marshes the submerged aquatic plants are limited, therefore not by the amount of sediment but by salinity (Penfound & Hathaway 1938, p. 44).

The writer is unaware of any publication which discusses the amount of sediment or duration of turbidity of the waters in the established marshes of the Central Gulf Coast or of the marshes of the lower delta. It has been estimated (Russell 1939) that under average conditions the Mississippi contributes 2,000,000 tons of sediment daily to its lower delta. This suspended material might in part be added to the established marshes of the alluvial plain if it were not for the high artificial or natural levees along the upper causeway. When the sediment-laden water at flood time reaches the active delta the newly formed, low levees allow it to spread over the marshes where deposition takes place. The building of a large spillway above New Orleans to produce an outlet into Lake Pontchartrain for river water during times of excessively high floods, means that never again will there be an inundation of the city and surrounding marshlands and swamps.

As previously noted, submerged plants are limited to the strictly fresh and slightly brackish conditions. With the exception of some algae, the salt lagoons or ponds are lacking in plant life. In the fresh marshes the open areas abound with vegetation which makes ideal breeding and protected areas for many Odonata, especially zygopterous nymphs. Of the submerged plants, the coontail (*Ceratophyllum submersum*) and bladderworts (*Utricularia gibba* and *U. macrorhiza*) are the most abundant; whereas the duckweeds (*Azolla caroliniana*, *Lemna minor*, and *Spirodela polyrhiza*), dissected liverwort (*Riccia fluitans*) and the white water lily (*Castalia odorata*) are the most important floating-leaved plants. In many marshes the open ponds are invaded by these aquatic plants. This greatly increases the area available for the vegetation-loving nymphs.

LIST OF SPECIES OF DRAGONFLIES FOUND  
IN THE ESTABLISHED MARSHES OF  
THE CENTRAL GULF COAST

Unfortunately, scant attention was given to the Zygoptera in our studies. It has only been since the summer of 1938 that any extensive collecting of damselflies has been done by us in this area. Our knowledge of the abundance and distribution of the Zygoptera, consequently, is but scanty and sporadic. The writer has published two papers (1937) and (1939), which list and give general information about the Anisoptera of the Central Gulf Coast Area. The salient information from these publications plus data obtained since 1938 are given in the following discussion.

1. *Agrion dimidiatum* Burmeister. A large series of this beautiful damselfly was taken at Rock Creek, Baldwin County, Alabama, on August 15, 1938. This is the only locality in which we have been able to find this species. Rock Creek is a typical agrionid stream in that it has a moderate flow, is spring fed, and flows through a heavily forested area. We were quite surprised to observe that *A. maculatum* was entirely absent in this area, as the latter species is abundant in such shaded creeks throughout the Central Gulf Coast.

2. *Agrion maculatum* Beauvais. A common inhabitant of clear, shaded streams throughout the area. This species usually flies within the confines of trees, but on several occasions individuals have been taken in the open, usually marshy, area.

3. *Hetaerina americana* Fabricius. This species is restricted to the same type of habitat as *Agrion maculatum* but has been rather rare in our collections. On several occasions individuals which correspond closely with the description of the variety described by Walsh—*Hetaerina a. texana*—have been taken or seen. In such cases the hind wings were almost completely red in color. These were very beautiful as they flew about or perched on the waterside vegetation. We have never observed this species in the open or marshy areas.

4. *Hetaerina titia* Drury. The only record of this species in our collection is from Bayou Lecombe Creek, St. Tammany Parish, Louisiana, July 2, 1938. Further collecting should show a wider distribution.

5. *Lestes disjunctus* Selys. Several specimens of this lestine were taken in the vicinity of a small pond at Mobile, Alabama, on July 1, 1938.

6. *Lestes vigilax* Hagen. Specimens of this large damselfly have been taken at Tehoutacabeeuffa Creek, Mississippi, on August 11, 1938; at Rock Creek, Baldwin County, Alabama, on August 15, 1938; and at Bay Minette Creek, Baldwin County, Alabama, on August 16, 1938. This is probably our most abundant and widespread lestine. *L. vigilax* was usually found only in swamp areas, but an occasional specimen was caught in the open. Our southern specimens of this species are larger than the northern forms that have been examined and show some differences in the elaspers of the male.

7. *Lestes vidua* Hagen. Hagen (1861) described this lestine and gave as its distribution New Orleans, Louisiana. We have not as yet found this species in the field.

8. *Argia fumipennis* (Burmeister). A common species along clear, well-shaded streams throughout the area. It will, upon occasions, wander into the nearby marshes or swamps.

9. *Argia moesta* (Hagen). This species was taken in the same areas as *A. fumipennis*, but never reached the abundance of the latter. Borror (1934) has shown that they fly some distance away from the stream.

10. *Argia tibialis* Rambur. Collections of this species were made at Bayou Lecombe Creek, St. Tammany Parish, Louisiana, on July 2, 1938; at Pearl River, May and June, 1938; and at Bay Minette Creek, Baldwin County, Alabama, August 16, 1938.

11. *Nehalennia irene* Hagen. Several specimens were taken along the Tehoutacabeeuffa River near Geean Springs, Mississippi, on August 11, 1938. This is our only record in the Central Gulf Coast.

12. *Enallagma durum* Hagen. This was one of the most common and widespread of our damselflies. It reached its greatest abundance in the brackish areas. Several nymphs were taken in Choceolotta Bay, Mobile, Alabama, on August 12, 1938, from among the *Pontederia* growing in the water. The females were usually found in the shaded areas and in patches of *Phragmites*, while the males perched in great numbers on the cattails (*Typha angustifolia*) and *Scirpus* and were captured in large numbers along the roadway.

13. *Enallagma pollutum* Hagen. We found this species in large numbers in the marshes in Bay Minette Creek Bay, Baldwin County, Alabama, on August 16, 1938. Further studies should show *E. pollutum* to be a common damselfly in our strictly fresh areas.

14. *Enallagma signatum* Hagen. Individuals of this species were found in a number of fresh water

localities. Additional collections will probably show this to be a very common fresh water species.

15. *Enallagma dubium* Root. Several mating pairs of this species were taken along the Tehoutacea-beeuffa River near Ocean Springs, Mississippi, on August 11, 1938. This is our only record.

16. *Enallagma concisum* Williamson. The only record of this species for the Central Gulf Coast is a mating pair collected by Mr. T. P. Hall, Tulane University, at Florencia, Louisiana, on May 15, 1938.

17. *Enallagma doubledayi* Selys. We have collected but three specimens of this damselfly, those from the water reservoir at Springhill, Mobile County, Alabama, during June, 1936.

18. *Ischnura prognatha* Hagen. A small number of specimens were taken during the summer of 1938 along the main lagoon in Audubon Park, New Orleans, Louisiana.

19. *Ischnura ramburii* Selys. This was one of the five most abundant damselflies in this area and was found in all marsh habitats. It and *Enallagma durum* were the only species of Zygoptera to be found in any abundance in strongly brackish and saline marshes. Pearse (1932) found nymphs of *I. ramburii* in pools where the salinity varied between 55 and 68 percent sea water.

20. *Ischnura posita* Hagen. Ranks with *I. ramburii* in spread and abundance with the exception of heavily brackish and saline areas, where *I. posita* was seldom found. The nymphs of this species are easily recognized and were taken frequently during this investigation. They were, however, found only in areas where either submerged or emergent vegetation was present.

21. *Anomalagrion hastatum* Say. This species was found throughout all types of marshes, but was never observed in any great abundance. One of our most interesting records was the capture of several individuals of *A. hastatum* in the salt marshes at Bayou La Batre, Mobile County, Alabama, on August 12, 1938. Until the nymphs of this species have been found in strongly brackish and saline areas, the writer will not accept this as a true salt marsh form.

22. *Gomphoides williamsoni* Gloyd. Nymphs and exuviae of this remarkably long-tailed gomphine have been taken from Audubon Park Lagoon in New Orleans, Louisiana, and from the Bayou des Allemands. Both of these localities are fresh areas, the latter body of water being bordered by extensive marshy areas. In spite of intensive searching no adults have been taken by the writer in this area. In the Bayou des Allemands area the nymphs were found to be buried in the muck along the shore, usually in the heavily vegetated area, while the exuviae were attached to the waterside vegetation. I am indebted to Dr. F. H. Wilson, Department of Zoology, Tulane University, for an adult female with its exuviae of this species which he caught at the time of transformation in Audubon Park Lagoon, New Orleans, Louisiana. In a letter to the writer

dated November 7, 1940, Dr. Wilson writes in regard to *G. williamsoni*, "The gomphoides records however are all right. The specimen which I gave Dr. Hathaway was caught at 11:30 P.M. July 3. It had just emerged from the exuviae and was wet. It was clinging to the exuviae which was on a stick projecting from about 5 inches of water. About a week later I found another one in the same condition as above, that is it had just emerged and was clinging to the exuviae which was on a board floating over about ten inches of water. Your specimen was found in the same location and condition as the latter. They were both found around 9:30 P.M." We have quoted this interesting information from Dr. Wilson because of the absolute lack of knowledge concerning transformation in *G. williamsoni*.

23. *Boyeria vinosa* (Say). The only record of this species in the Central Gulf Coast is from Rock Creek, Baldwin County, Alabama, on August 15, 1938.

24 and 25. *Anax junius* Drury and *Coryphaeschna ingens* Rambur. These two "darners" were common throughout the entire area. They are strong fliers and are capable of ranging throughout the area. A huge swarm of *Anax junius* adults was observed in the salt marshes at Bayou La Batre and along Coden Bay, Mobile County, Alabama, during the summer of 1938. We have frequently observed both species swarming just before dusk. At Pearl River, Louisiana, during September, 1940, the writer estimated some two hundred *Coryphaeschna ingens* in a mass dashing after the gnats and small tipulids which were present by the millions. The "darners" moved down the road for about half a mile before they, disturbed by approaching automobiles, "zoomed" high into the air and disappeared into the woods. The nymphs of *A. junius* are true climbers and we have always found them closely associated with vegetation. Large numbers of *Anax* nymphs have been collected in the *Typha* zones bordering open bodies of water. Both nymphs breed—in so far as our data indicate—only in fresh or slightly brackish conditions.

26 and 27. *Nasiaeschna pentacantha* Rambur and *Epiaceschna heros* Fabricius. These "darners" were much less abundant than the previous two and have been but rarely observed in the brackish and saline areas.

28. *Perithemis tenera* Say. Our data indicate that this species is confined to fresh or very slightly brackish areas. They were found on or near bodies of slowly-moving water where they mated and oviposited. Oviposition was noted in several cases, always occurring in algal mats. Collections made since 1937 indicate that this species has a much wider distribution than then indicated (Wright 1937). *P. tenera* inhabits nearly all of our large ponds, lagoons, lakes, and has even been found in fresh marshes.

29. *Celithemis eponina* Drury. One of the common species of this area, being found from fresh

to almost saline areas. It was usually found only in the marsh, often perching on the *Phragmites* cane. During the middle of the summer the vast cane areas of the brackish marshes appeared as if every stalk had an individual of this species on it. Very few nymphs have been taken during this study, so no knowledge as to its breeding habits is available.

30. *Celithemis fasciata* Kirby. A rare species during our investigation. When captured, it was in company with *C. eponina* in fresh and slightly brackish marshes.

31. *Celithemis amanda* (Hagen). A considerable number of adults were seen and a series collected in the marshy areas bordering Bay Minette Creek, Baldwin County, Alabama, on August 16, 1938. The writer had considered this to be restricted to fresh water areas until he caught several adults during the summer of 1940 in the brackish marshes along the Mobile Bay Bridge Road in Alabama.

32. *Erythrodiplax berenice* Drury. This species can truly be said to be restricted to brackish and salt marshes. Our collections show that its relative abundance increases with the increase in salinity. The investigations of Pearse (1932) show that this species can survive in waters with a salinity more than one and one half that of sea water. In spite of the abundance of the adults the writer has never succeeded in finding the nymphs of this species, although many hours have been spent in the attempt. This was probably in part due to the tremendous acreage of salt and brackish marsh.

33. *Erythrodiplax minuscula* Rambur. This species was taken in the dry marshy areas of the Cat Island in the Mississippi Sound during the spring of 1933, and in the marshes near Pearl River, Louisiana, during September, 1940. This was a rare species according to our data, although further collecting may prove otherwise.

34. *Orthemis ferruginea* Fabricius. This species appeared during the latter part of the summer, and was found only around fresh water areas or in the surrounding fields and woodlands. They were quite agile, flew from their perches at one's approach and very seldom returned to the same place.

35. *Libellula auripennis* Burmeister. This was the most common and the most widely distributed of the species found in the Central Gulf Coast. The adults were found from the most salty conditions to the least salty and from the flats and marshes to the forests and swamps. During the middle of the summer in the fresh and brackish marshes in the vicinity of New Orleans they congregated in vast swarms, and even penetrated into the city in clouds.

36. *Libellula semifasciata* Burmeister. Adults were taken at Mobile, Alabama, June, 1937; swamp at Pearl River, Louisiana, May 1, 1938; and at Florencia, Louisiana, May 15, 1938. This was a very rare species in our area.

37. *Libellula pulchella* Drury. Specimens have been taken at Mobile, Alabama, during July, 1934, while flying over and ovipositing in a drainage ditch,

and in the fresh marshes along the west side of Lake Pontchartrain on several occasions. This species and *L. semifasciata* were rare in the Central Gulf Coast but became more abundant further north. No nymphs of *L. pulchella* were taken during this investigation, but the writer has collected a large number in the vicinity of Nashville, Tennessee, and Columbus, Ohio. They were taken in every case in marshy areas of ponds or small lakes.

38. *Libellula inesta* Hagen; 39. *Libellula vibrans* Fabricius; and 40. *Libellula axillena* Westwood. Until the spring of 1938, *L. inesta* and *L. axillena* were considered to be the same as *L. vibrans*. The writer is indebted to Mrs. Leonora K. Gloyd who not only called his attention to the distinctness of these three species but also for her kindness in sending an excellent series of characters for their separation. Field collecting since then has shown that these species are very similar in habit. They are shade-loving forms, and were only occasionally taken in open areas. They seemed to be the most sluggish of the libellulids in our area. One could approach to within several inches of them before they slowly flew away, frequently returning to the same perch. It was not at all unusual to be able to catch *L. vibrans* by hand if care was taken not to make a loud noise while approaching. It, according to our investigation, was by far the most abundant of the three; in certain areas it became exceedingly numerous. *L. inesta* ranked second of the group in abundance, while as yet we have found *L. axillena* to be somewhat rare.

41. *Plathemis lydia* Drury. This was a very common dragonfly in its restricted habitat. They were taken only in fresh or slightly brackish situations. *P. lydia* seemed to prefer small lakes or ponds with mucky bottoms for their ovipositing. Many nymphs of this species have been collected and always from such areas. The nymph is able to withstand a considerable amount of stagnation and pollution. On several occasions we have found nymphs of *P. lydia* in pools in which, on account of loss of water, decay had progressed to such a point that an oil scum had formed on the surface of the water. The adults were usually found near the breeding areas, but they often ranged long distances into the surrounding woodlands and marshes.

42. *Cannacria gravida* Calvert. This dragonfly was found in all types of marshes, but predominated in brackish areas. At certain times during the summer large numbers were observed, but more often among the other species present *C. gravida* ranked fourth or fifth in abundance. It was an almost constant companion of *Libellula auripennis* and *Celithemis eponina* in the marshes, and, like them, was found in large numbers perching on the roseau canes (*Phragmites*). *C. gravida* was one of the five most common species of dragonflies in the Central Gulf Coast marshes.

43. *Tarnetrum corruptum* (Hagen). A sturdy flier, found in or near woodlands or overgrown fields

surrounding bodies of fresh water. This species appeared as early as April and lasted throughout the summer. It never became abundant in any area investigated.

44. *Sympetrum ambiguum* Rambur. This was a late summer species and rarely was found other than in well-shaded areas. It was found in shallow streams or ponds or over their dried beds where overhanging trees formed a continual shade. The males flew slowly over the tops of the weeds in these shaded areas, frequently perching for short periods of time. The brown-spotted female darted rapidly about attracting the males. The writer has frequently seen five or six males attending one female. Finally, one would clasp the female and fly rapidly away. Copulation took place while the pair were flying and perching. No oviposition was observed by the writer.

45. *Pachydiplax longipennis* Burmeister. This species ranked as one of our most common and widely distributed species. It was found in the same areas as *Libellula auripennis*, but never reached the extreme numbers of the latter.

46. *Erythemis simplicicollis* Say. Very similar in habitat and abundance to *Pachydiplax longipennis*; at times it almost reached the abundance of *Libellula auripennis*. In the discussion of factors affecting dragonfly nymphs, the nymphs of this species have been shown to be able to survive in many different types of habitats. We have not, however, as yet taken nymphs in strongly brackish or saline marshes, although the adults were present in large numbers.

47. *Pantala hymenaea* Say. In all this study there has been but one specimen of this species taken, and that at Mobile, Alabama, during September of 1935.

48. *Pantala flavescens* Fabricius. A not uncommon species of the late summer and fall. They were found around bodies of fresh water, forest lands, open grassy fields, and occasionally were taken in brackish water areas.

49. *Macrodiplos balteata* (Hagen). Our only collections were made at the Fish Hatchery at LaCombe, Louisiana, on July 2, 1938; and on Petit Bois Island off Biloxi, Mississippi, on July 15, 1938. The capture of these specimens in Louisiana is of considerable interest as the species has been known, according to Needham and Heywood (1929), only from southern Texas and the Florida Keys. The writer is confident that further collections in the Gulf Coast will show this species to be more common than is herein indicated.

50 and 51. *Tramea lacerata* Hagen and *T. carolina* Linn. These two species have an identical distribution, but *carolina* was by far the most abundant. They were found in every habitat, and appeared in large numbers in the brackish areas. The writer observed large numbers of *T. carolina* flying over or perching on the vegetation at the edge of the beach at Coden Bay, Alabama, which is an arm of the Gulf of Mexico and is bordered by saline marshes.

When approached, *T. carolina* would fly rapidly away, then return to its perch, fly slowly around and, if the observer made no motion, would realight. The writer has watched individuals perform these movements as many as five times before moving to another perch. When frightened, however, they darted rapidly upward until sufficiently removed from danger, and would then seek another perch.

#### ANALYSIS AND COMPARISON OF THE DRAGONFLY POPULATIONS STUDIED

A detailed study of the Odonate populations of the two areas investigated gives some interesting information as to the species therein and, in addition, shows in what respect the populations differ. The established marshes of the Central Gulf Coast will be considered first as they represent the basic type and illustrate the form which will occur in the delta as the given marsh becomes sufficiently isolated from the active portion. Table 4 presents a general analysis

TABLE 4. Analysis and comparison of dragonfly populations of the area studied.

Number of Species	In Central Gulf Coast Marshes	In Lower Mississippi River Delta Marshes
Agrionidae.....	4	0
Lestidae.....	3	0
Coenagrionidae.....	14	3
Total Zygoptera.....	21	3
Gomphidae.....	1	0
Aeschnidae.....	5	2
Libellulidae.....	24	8
Total Anisoptera.....	30	10
Total Odonata.....	51	13
Generally restricted to wooded areas.....	16	1
Restricted to fresh areas exclusive of wooded areas.....	15	4
Restricted to saline areas.....	1	1
Found in both fresh and saline areas.....	19	7
Common species in marshes.....	19	5

and comparison of the Odonate populations of the two areas.

In the established marshes we have recorded 51 species, of which 21 are Zygoptera and 30 are Anisoptera. All three families of damselflies are represented therein, but only three of the Anisopterous groups have been found. The writer has never taken members of the Petaluridae, Cordulegasteridae, Macromiinae, or Corduliinae in any of the marshes or swamps of this area. In the pine lands, which are located just north of the coastal marshes and through which run a number of clear, cold streams, we have taken representatives of the groups.

The various species of dragonflies in this area fall into four groups in regard to their distribution: (1) species generally restricted to the wooded areas; (2) species restricted to fresh areas other than

woods; (3) species restricted to saline areas; and (4) species inhabiting both fresh and saline areas. We are using the terms fresh and saline here in their broader sense, in that the fresh areas include strictly fresh and slightly brackish marsh, while saline areas include brackish as well as salt marshes. As adult dragonflies are sturdy fliers in the majority of species and obtain their food while on the wing, they cannot be limited absolutely to a single definite habitat type. Many species do, however, show strong preferences for a particular environment and are usually restricted to such areas.

There were 16 species of dragonflies in the established areas which were usually restricted to the surrounding or nearby wooded regions. These were found upon occasions, in the open, but they usually inhabited the well-shaded areas. The wooded regions are of two general types: swamps and bogs, and pine or oak forests through which run clear creeks. Such dragonflies as *Libellula vibrans*, *L. incesta*, and *L. axillena* were taken in both situations. The lestines, *Lestes disjunctus* and *L. vigilax*, were usually found in swampy or boggy areas served by a clear creek. *Boyeria vinosa* adults were taken in swamps, but the nymphs were found only in a small clear stream flowing through the edge of the swamp. The following species were usually found only along the clear streams: *Agrion dimidiatum*, *A. maculatum*, *Hetaerina americana*, *H. titia*, *Argia fumipennis*, *A. tibialis*, *Nehalennia irene*, and *Sympetrum ambiguum*. The damselfly *Lestes vidua* is tentatively included in the list of shade-loving species as the other lestine species found in this area were of this type. Our knowledge of the abundance and distribution of the genus *Lestes*, as well as the Zygoptera as a whole, in the coastal marshes is quite scanty. Further collecting will undoubtedly produce many additional species and give more data on those forms listed herein.

According to our data, there were 15 species restricted to the fresh water areas. In this the dragonflies of the wooded areas discussed above are excluded. The fresh areas included marshes, ponds, and pools, unshaded creeks and bayous. The bodies of open water are usually well populated with aquatic plants and in a great many cases have a distinct marshy border. The Zygoptera found herein, *Enallagma pollutum*, *E. signatum*, *E. dubium*, *E. concisum*, *E. doubledayi*, and *Ischnura prognatha*, were taken only in the marshy areas bordering streams or ponds. *Gomphoides williamsoni*, the only gomphine as yet found in this area, was taken in like situations. *Perithemis tenera*, *Plathemis lydia*, *Orthemis ferruginea*, and *Tarnetrum corruptum* were small lake-pond species which, however, might invade various of the fresh water types. *Libellula semifasciata* and *L. pulchella* were quite rare during this investigation but, from observations in other areas, they are probably marshy pond species. On account of our lack of knowledge of both breeding requirements and adult

distribution, we have included in this area *Pantala hymenaea* and *Macrodiplex balteata*.

*Erythrodiplax berenice* was the only species during these studies that was found to be restricted to the saline areas. The collections, moreover, show that the abundance of this species was greatest in those areas in which the salt concentration was highest. Several investigators have made reference to the ability of *E. berenice* to live in areas having high salinities. Osburn (1906) as a result of his study of the effect of salt water on dragonfly nymphs concluded, ". . . it may be that forms such as *Micrathyria berenice* which are limited in distribution to the coast lines have a higher limit than those species which occur in the interior only." Pearse (1932) took nymphs of *E. berenice* from a pond in which the salinity varied between 55 and 68 percent sea water, and from a pool varying from 157 to 170 percent sea water. Such data indicate that this species is able to survive in the most saline marshes of the Central Gulf Coast.

There were 19 species, however, which were found as adults in both fresh and saline marshes. They are: *Enallagma durum*, *Ischnura ramburii*, *I. posita*, *Anomalagrion hastatum*, *Anax junius*, *Coryphaeschna ingens*, *Nasiaeschna pentacantha*, *Epiaceschna heros*, *Celithemis eponina*, *C. fasciata*, *C. amanda*, *Erythrodiplax minuscula*, *Libellula auripennis*, *Cannacria gravida*, *Pachydiplax longipennis*, *Erythemis simplicicollis*, *Pantala flavescens*, *Tramea lacerata*, and *T. carolina*. The collecting of dragonfly nymphs throughout this area over a long period of time led us to conclude that the majority of listed species bred in the fresh areas and due to their excellent flying ability migrated into the saline areas. That some of these species must have been able to breed in brackish areas is shown by the data obtained in the active delta marshes.

The large numbers of dragonflies made this group one of the most conspicuous elements of the fauna of the Central Gulf Coast, yet it is extremely difficult to picture to someone who has never worked in this area the numbers of individuals of the various species observed. There were, however, certain dominant species which will be listed here. In the wooded areas the most abundant species were *Libellula vibrans*, *L. incesta*, *Agrion maculatum*, and *Argia fumipennis*. In the fresh water areas, excluding the marshes, the most frequently observed dragonflies were *Perithemis tenera*, *Plathemis lydia*, and, in the fall, *Tarnetrum corruptum*. The dominant species of dragonflies of the marshlands, with the exception of *Erythrodiplax berenice*, were found in all types from fresh to saline. They were, in order of decreasing abundance, *Libellula auripennis*, *Erythemis simplicicollis*, *Pachydiplax longipennis*, *Erythrodiplax berenice* (salt only), *Cannacria gravida*, *Celithemis eponina*, *Tramea carolina*, *Anax junius*, and *Coryphaeschna ingens*. The zygoterous species *Ischnura ramburii*, *Enallagma durum*, *Ischnura*

*posita*, and *Anomalagrion hastatum* were the most abundant of this group in the marshes.

In the lower delta of the Mississippi River, the list of species was but 13, of which 3 were Zygoptera and 10 were Anisoptera. One species, *Libellula vibrans*, was restricted to the wooded areas occurring on the deltaic ridges. This area cannot be divided into areas which are constantly fresh or saline, but certain regions (Table 3) remain fresher than others, even during the salt inundation. Only in such areas were the following dragonflies observed: *Anax junius*, *Coryphaeschna ingens*, *Celithemis eponina*, and *Tramea carolina*. *Erythrodiplax berenice* was restricted to those marshes having high salinities. The remaining seven species were taken throughout the various marsh types.

Dragonflies in the lower deltaic marshes, as in those of the Gulf Coast, are extremely numerous as individuals. One of the most interesting facts that developed from this investigation of the deltaic marshes was that probably over 90 percent of the individuals observed or captured in this area belonged to the following five species: *Libellula auripennis*, *Cannacia gradata*, *Erythemis simplicicollis*, *Pachydiplax longipennis*, and *Erythrodiplax berenice*. The remaining eight species were quite rare, only a relatively few specimens of each being seen during the study.

A comparison of the two populations shows that the five species which were abundant in the deltaic marshes were also among the most common forms in the established coastal marshes. This evidence leads the writer to conclude that these species are able to become acclimated to the great variation of salinity of the delta, and, undoubtedly, are able to breed in strongly brackish areas in the coastal marshes.

#### DISCUSSION

The foregoing discussion presents several important facts which are explainable on the basis of ecological factors. These facts are: (1) The presence of large numbers of individual dragonflies in the established marshes of the Central Gulf Coast; (2) the presence of only 13 species of dragonflies in the lower delta of the Mississippi River; (3) the presence of large numbers of individuals of the 5 successful species in the lower delta.

(1) The presence of large numbers of dragonflies in the established marshes of the coastal area can be explained readily by a review of the habitat factors of these marshes. The Central Gulf Coast contains several million acres of marshland, the majority of which remains under water throughout the year. There are, in addition, many areas of open, permanent water, which afford excellent breeding places for dragonflies. These marshes include both fresh and saline areas which, though they vary in salinity, do so within restricted limits characteristic of each type. Aquatic plants are present in the open fresh areas and even in the fresh water marshes, thus

producing the conditions necessary for the vegetation-loving nymphs and for those adults that exhibit endophytic oviposition. The temperature is ideal in that there is less than a 30° F. difference between the average winter and summer readings. The normal precipitation is in the neighborhood of 60 inches per year, and is evenly distributed throughout the year, which produces a steady, constant addition to the marshlands. Food is abundant and at all times available for both adults and nymphs. Even though there are large numbers of dragonflies, and these insects do eat considerable numbers of both larval and adult mosquitoes, the latter become serious pests in many of the southern marshes. Thus, these factors which make for the propagation of dragonflies are abundantly present in this area. Hence, any species whose nymphs are marsh, pond, or bayou inhabiting forms, in spite of enemies, is able to reach its maximum under such conditions.

(2) The restriction of the Odonate population of the lower delta to 13 species as against 51 species (and undoubtedly more), in the coastal marshes, is due to (a) the annual variation in salinity, and (b) the turbidity of the water.

As has been previously explained, the delta undergoes an annual fresh water and an annual salt water inundation. This has two important effects upon the delta. First, the forests or wooded areas are restricted to the higher deltaic ridges where they are removed from the effect of the salt water inundation. Thus, swamps are absent throughout the lower delta and the amount of forest is very small. This accounts for the presence of only one shade-loving species and for its rarity. As the delta progresses gulfward the inner portions will become isolated from the salt water action. At such a time swamps will appear and with them will occur an influx of the wooded-area forms which are now present in the coastal region. The second effect of the variation in salinity is the changing of the fresh marshes to brackish marshes, and the salt to relatively fresh marshes. This means, then, that any dragonfly—or other true aquatic insect—able to survive in these areas must be able to withstand this tremendous yearly change in salinity with the resulting change in osmotic pressure. It is this factor that we believe is of major importance in accounting for the fact that five of the species present in the lower delta form about 90 percent of the Odonate population.

The waters of the lower delta, as previously stated, with the exception of the protected pools, are extremely turbid. This results in the total absence of both submerged and floating plants in such areas which are brought about by the prevention of sunlight reaching the plants in a quantity sufficient for photosynthesis. Thus, those dragonflies, the nymphs of which are closely affiliated with aquatic vegetation—the majority of the Zygoptera and many of the Aeschninae—are unable to survive. The presence of such species of damselflies in the delta is due, as pointed out before, to the inside ponds which as a

result of their isolation from the passes and bayous are plentifully supplied with aquatic plants. The "darners" might have bred in these ponds, but on account of their strong flying ability, they probably migrated in.

In the course of these studies the possible deleterious effect of turbidity on the respiration of dragonfly nymphs suggested itself, but no investigations have been possible to determine this point.

(3) The presence of large numbers of individuals of the five successful species in the lower delta is due to the fact that any species of Odonata which is able to be acclimated to the saline variation and is not dependent upon aquatic vegetation finds the remaining factors, as in the coastal marshes, ideal for its propagation.

The five successful species of the lower delta marshes as well as the most abundant dragonflies of the coastal marshes are members of the Libellulinae. The nymphs of these species, as is typical of the subfamily, are mud sprawlers; that is, they are able to live on the bare mud or muck bottom and are not dependent upon aquatic vegetation. Since the greater part of both the areas studied have a mucky bottom, this characteristic of the nymph is of great importance not only in determining those species which could survive therein, but also in the production of large numbers of individuals of a given species. Thus, any dragonfly whose nymph is a true mud sprawler has almost unlimited breeding and feeding grounds. Those species with vegetation-loving nymphs are restricted to the areas supplied with aquatic vegetation.

I am surprised to note the presence of but a single species of Gomphidae in the coastal area. The majority of the species of this family have nymphs which are burrowing forms. These nymphs bury themselves in the mud and by means of the usually elongated posterior end are able to make contact with the overlying water. The gomphine found in the coastal region, *Gomphoides williamsoni*, possesses an elongated tenth abdominal segment almost equal in length to the other nine segments. The conditions in which this species was found was seemingly favorable for gomphine development, in that the bayou has a mucky bottom, its waters are clear of sedimentation during the greater part of the year, and there are numerous waterside plants suitable for transformation. In such conditions elsewhere, the writer has found numbers of gomphine nymphs and adults. We are not able, at present, to explain the absence of all but one species of this family in the Central Gulf Coast.

#### SUMMARY

1. The purpose of this paper is to compare the dragonfly population of the large areas of the established marshes of the Central Gulf Coast with that of the lower active delta of the Mississippi River.

2. The Central Gulf Coast contains several million acres of marshland, the majority of which re-

main under water throughout the year. There are many acres of open permanent water which afford excellent breeding places for dragonflies. These marshes include both fresh and saline areas which, though they vary in salinity, do so within restricted limits characteristic of each area. Aquatic plants are present in the open fresh areas and even in the fresh water marshes, thus producing conditions necessary for the vegetation-loving nymphs and for those adults with endophytic oviposition. Temperature conditions are ideal in that there is less than a 30° F. difference between the average winter and summer readings. The normal precipitation is in the neighborhood of sixty inches per year and is evenly distributed throughout the year, thus producing a steady and constant addition to the marshlands. Food is abundant and at all times available for both adults and nymphs.

3. The marshes of the lower delta of the Mississippi River enjoy the same climatic and biological factors as the Coastal Marshes, but differ from the latter in two major physical factors:

(a) *Salinity.* The delta undergoes an annual fresh-water and an annual salt-water inundation, which have two important effects on the delta. First, the forest or wooded areas are restricted to the higher deltaic ridges where they are removed from the effect of the salt-water inundation. Thus, swamps are absent throughout the lower delta and the amount of forest is very small. The second effect of the saline variation is the changing of the fresh marshes to strongly brackish marshes, and the salt to slightly brackish marshes. This means that any aquatic insect able to survive in these areas must be able to withstand this tremendous saline change. It is this factor that is probably of major importance in accounting for the fact that five of the species present in the lower delta form about 90 percent of the Odonate population.

(b) *Turbidity.* The waters of the lower delta, with the exception of the outside and inside pools are extremely turbid. This results in the total absence of both submerged and floating plants, due mainly to the reduced amount of sunlight (necessary for photosynthesis) penetrating the water. Thus, those species of Odonata the nymphs of which are closely affiliated with aquatic vegetation (the majority of the Zygoptera and many of the Aeschninae) are unable to survive. The presence of such species in the delta is due to the inside ponds which, as a result of their isolation from the passes and bayous, are plentifully supplied with aquatic plants.

4. In the Central Gulf Coastal marshes 51 species of Odonata were recorded, of which 21 were Zygoptera and 30 were Anisoptera. The various species found in this area fall into four groups in regard to their distribution:

(a) *Wooded area species.* Sixteen species were found to be restricted to wooded areas, which in

this area were of two types: swamps and bogs; and pine or oak forests through which run clear creeks.

(b) *Fresh-water species*. Fifteen species were restricted to fresh-water areas. This number does not include the species of the wooded areas mentioned previously. Fresh areas include marshes, ponds, pools, unshaded creeks and bayous.

(c) *Saline area species*. The only species found to be restricted to saline areas was *Erythrodiplax berenice*. The abundance of this species was greatest where the salt concentration was highest.

(d) *Fresh-saline area species*. Nineteen species were found as adults in both fresh and saline marshes. It is probable that the majority of these breed in fresh areas and migrate into the saline areas; however, the data obtained in the active delta show that some of these must be able to breed in brackish areas.

5. In the marshes of the lower delta of the Mississippi River only thirteen species of Odonata were found, three Zygoptera and 10 Anisoptera. Approximately 90 percent of the individuals observed or captured in this area belonged to one of five species: *Libellula auripennis*, *Cannacia gravida*, *Erythemis simplicicollis*, *Pachydiplex longipennis*, and *Erythrodiplax berenice*.

6. The restriction of the deltaic Odonate population to thirteen species of which five compose 90 percent of the population is apparently due to: (1) the considerable annual variation in salinity; and (2) the excessive turbidity of the water.

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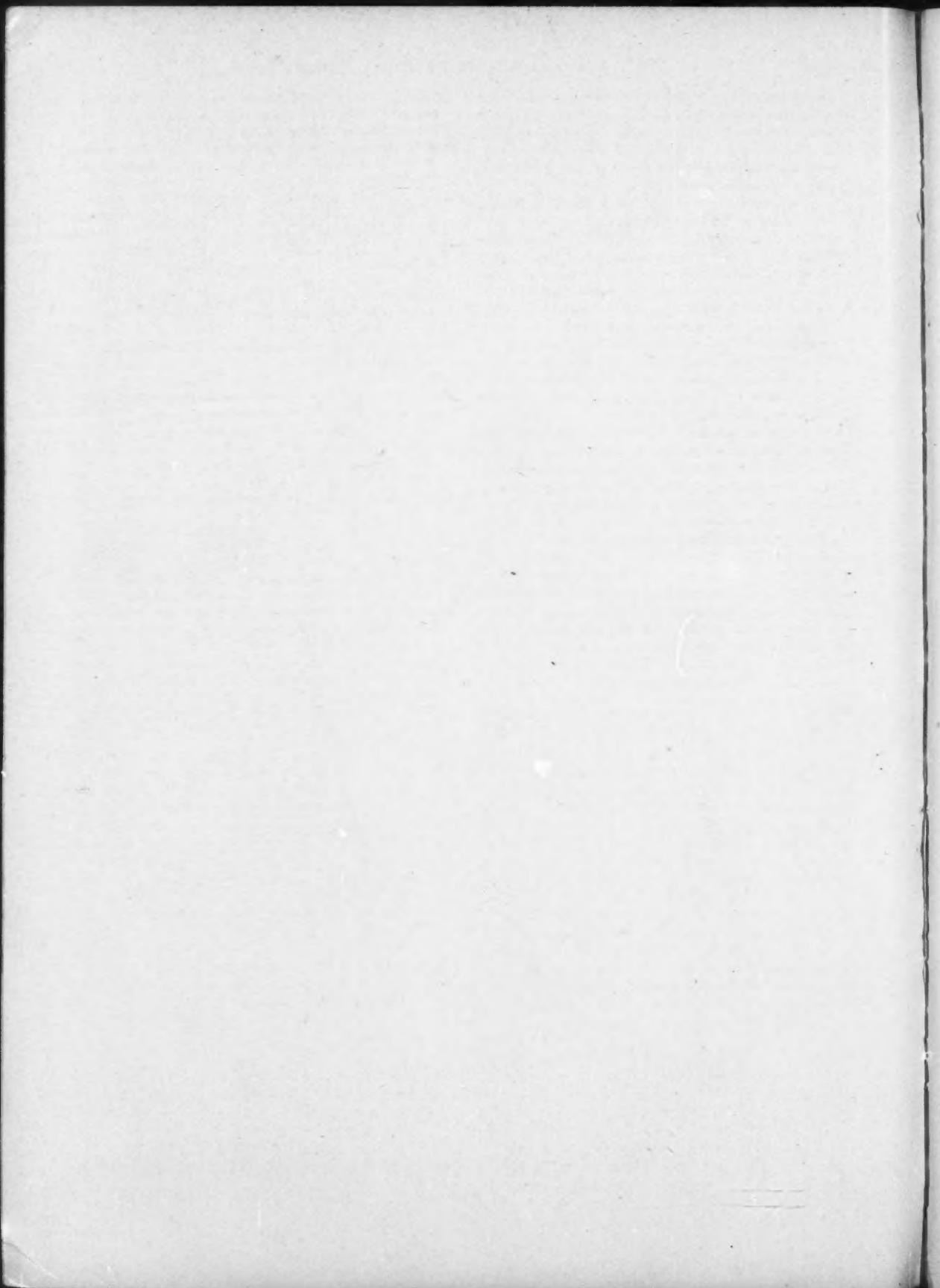
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